Management of Soil, Nutrients and Water in Tropical Plantation Forests

Editors

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Published by
ACIAR
Australian Centre for International Agricultural Research
In collaboration with
CSIRO Australia
Commonwealth Scientific Industrial Research Organisation
and
CIFOR Indonesia
Center for International Forestry Research

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GPO Box 1571, Canberra ACT 2601, Australia

Nambiar, E.K. Sadanandan, and Brown, Alan G. 1997. Management of Soil, Nutrients and Water in Tropical Plantation Forests. ACIAR Monograph No. 43, xii + 571 p.

ISBN 1 86320 198 X

Front cover: A plantation of hoop pine (*Araucaria cunninghamii*) in Queensland, Australia. These plantations are managed for high value solid timber production over rotations of up to about 60 yr; their understorey is rich in biodiversity.

Back cover: A plantation of *Eucalyptus grandis* in Brazil. Such plantations are managed on short rotations (8–11 yr) for pulpwood production.

Editorial management: P.W. Lynch
Design, typesetting and layout: Arawang Pty Ltd, Canberra, Australia
Cover design: Vlad Mosmondor, CSIRO, Canberra, Australia

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Preface

PLANTATION FORESTRY in the sub-tropics and tropics is already extensive and is expanding rapidly. The benefits of successful ventures have been economic, environmental and social, and there are many more opportunities as well as needs for its further development. The sometimes disappointing outcomes may be attributable to a wide range of factors— bio-physical, managerial, economic or political.

This book is largely about the bio-physical issues that determine productivity of plantation forests. Its genesis was our conviction that the sustainable management of plantation forests in temperate regions of the world, and understanding of how plantations grow in the long term, have improved greatly over recent decades. Here was an opportunity to foster the development of corresponding knowledge and its application to plantations in the sub-tropics and tropics, the productivity and sustainability of which have often raised questions.

The precursor to this book was an earlier text (*Nutrition of Plantation Forests*, G.D. Bowen and E.K.S. Nambiar, ed. 1984, Academic Press, London) which provided an holistic analysis of soil and eco-physiological factors of production, especially in temperate ecosystems.There have been several other detailed treatises on temperate plantation ecosystems but few on tropical plantations.

The literature flowing from recent and current research on afforestation in tropical countries and our experience in the field indicated to us a serious lack of the holistic approach required to provide enduring solutions to field problems and to promote sustainable plantation forestry. Research in various disciplines must be planned and undertaken interactively, and researchers and managers should have a keen sense of the interrelationships of ecosystem processes, function and management to achieve optimum progress.

The diversity of the physical and biological characteristics of plantations in the sub-tropics and tropics is immense, as also is the variation in management practices in the field. No single text can fully address such variation and arrive at a simple synthesis. We were cognisant of this in planning the scope of this book.

The aim of this book then is to improve understanding of how soil, water and nutrients can be better managed for increasing and sustaining production in tropical regions with due care for the environment. To achieve that aim we need to understand the opportunities and constraints that occur at various levels in the ecosystem and how management practices may affect them. We also should recognise that plantation forestry needs to be profitable. The book is not designed to be a practical guide or prescription for managers, but an effort to relate information on processes to field problems and potential solutions which might be pursued by innovative management. The focus is on the use of plantation forests as a valuable land use. Although agroforestry is an expanding land use in the tropics, the scope of the book did not permit explicit attention to agroforestry systems.

The first chapter sets the scene for the book with an examination of the role, extent and nature of plantation forests. Chapters 2, 3 and 4 describe the nature of the resource base: genetic, bio-physical and soil respectively. Chapters 5 and 6 analyse the dynamics of hydrology, and the closely related issues of leaf and crown development. Chapter 7 describes the physiological processes of growth, which are dependent on the availability of light, water and nutrients. The root systems of trees often consume a large fraction of the assimilate fixed by photosynthesis; their development and function is summarised in chapter 8. Nutrient supply is often the factor most limiting plantation growth: chapter 9 examines biological nitrogen fixation in plantations, while broader aspects of the dynamics of nutrient cycling and the effects of management on it are discussed in chapter 10.

Management practices can do much to squander, conserve or improve soil resources in plantations: management options for intensive production of short-rotation plantations and consequences of repeated cropping are considered in chapter 11. The dynamics of stand growth, and options for the manipulation of factors which affect it, are considered in chapter 12. In chapter 13, the role and fate of organic matter, with which critical nutrient reserves are associated, is described and discussed. Soils which have been degraded, either by natural factors or poor land management in the past, are often encountered in potential sites for plantations. The problems these soils pose, and the prospects for growing successful tree crops on them, are considered in chapter 14. Chapter 15 raises and discusses the diverse perceptions of sustainable management and gathers salient points from the preceding discussions, and argues that much information and many of the techniques developed through research in temperate plantations provide a basis for action in the challenging environments of the tropics. Attention is drawn to the need to ensure that plantation forests bring overall economic and social benefit to the communities in which they may be located; their biological success is essential but not sufficient for this. It points out the need for setting the goals of management in appropriate bio-physical, economic and social contexts, and identifies the constraints for developing and implementing effective research strategies for pursuing sustainability.

The authors who contributed to this multi-disciplinary text have diverse backgrounds, and as editors we have endeavoured to accommodate their experience, ideas and interpretations as much as possible. Important areas for future research are identified in each of the chapters.

We hope this book will assist people taking up research on productivity of sub-tropical and tropical plantations, advanced graduates and post-graduate researchers, and especially scientists in national and international research organisations planning to re-orient their research. It may be particularly useful to those who, while being specialists in their own area (e.g. water or nutrition or physiology) seek a balanced knowledge of broader bio-physical topics related to their work. The need to stimulate such an outlook in current and future research for sustained productivity is indeed one of the prime motives for producing this book.

We are grateful to many people for assistance in accomplishing this task: to all contributing authors for their commitment to the project and for overcoming with us the well-known pitfalls that lurk in multi-authored ventures; to the Australian Centre for International Agricultural Research (ACIAR), Canberra, Australia for partly sponsoring this project, and especially to Peter Lynch for undertaking the major task of publication; to the Center for International Forestry Research (CIFOR), Bogor, Indonesia for partial sponsorship and encouragement, and for the special contribution of Christian Cossalter in organising a workshop of authors at the planning stage; and to CSIRO, our employer, for backing this project through all stages. Other colleagues within CSIRO Forestry and Forest Products and internationally have generously helped us through discussions, the supply of information, reviews and encouragement. We thank them all.

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Plantations for the Tropics—Their Role, Extent and Nature

A.G. Brown
E.K.S. Nambiar
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Abstract

This chapter describes the context in which tropical forest plantations are expanding as a source of industrial wood and fuel. World demand for the former is increasing, but the rate of increase is slowing and is subject to fluctuations in economic activity. Dependency on fuelwood is very high in many countries, and is not lessening overall. The use of planted trees by communities and industry to satisfy these demands is increasing. A small number of species have been very widely used, but there is merit in extending the choice available to growers, in part to better cater for the diverse biophysical and socioeconomic environments in tropical countries. The very varied climates and soils of the tropics are reflected in great variation in plantation yield, and there are many critical issues yet to be understood regarding sustainable production by tropical plantations. Several factors which cause low productivity are amenable to manipulation by managers. Experience from temperate regions can provide valuable guidance for both practice and research in the tropics. Wood requirements cannot be satisfied from native forests alone; plantations offer proven prospects for higher rates of production per unit area compared to native forests, and the production trend suggests that even forest-rich nations are shifting their reliance for wood supply from native forests to plantations. Long-term production with requisite environmental care is a challenge for both research and practice.

TREES HAVE been planted for domestic purposes for many centuries. Productive home gardens containing a mixture of species are common in many tropical countries, although the pressure to subdivide and allocate more of the already small area of family land to housing and other purposes as the numbers of family members increase has resulted in a dwindling number of trees, especially of timber species, in these gardens. In temperate regions larger-scale plantings for industrial products, typically of a single species, have greatly expanded in the 20th century. Now plantings in the tropics for both domestic and industrial purposes are rapidly increasing. This increase has been prompted by the reduced availability of wood from native forests because of their conversion to agriculture or overcutting or conservation needs, and the prospect that plantations can supply large volumes of wood of uniform quality well suited to industry, especially for paper-making. In some instances changes in land tenure or markets make wood production attractive for small-holders, while in others the value of plantations in providing shelter or other amenity has been significant.

Plantations and associated processes are often compared unfavourably with undisturbed tropical forest (e.g. Dudley et al. 1995). Sedjo and Lyon (1990) emphasise that most plantations in the subtropics are on lands that have not been forested in recent years, or in cases such as the tropical Orinoco River Basin, in recent centuries. Thus in many cases a more appropriate comparison is with forms of land cover which do not include trees, such as imperata grassland or with slash-and-burn agriculture. These forms of land use are sometimes a consequence of land tenure arrangements which, if suitably modified, would result in the regeneration and care of indigenous forests, as has been happening in Nepal (McLaughlin 1996). Plantations may provide an initial impetus for this process. In some situations, harsh environmental conditions limit options to foster development of alternative vegetation, for example along the coastal dunes of southern China where casuarina has been used for a very extensive shelterbelt. There is evidence from Australia and elsewhere that tree plantations can play an important role in improving the environment by mitigating land degradation. In many cases, plantations are the most feasible way of providing wood for expanding household and industrial needs. Shepherd (1993) provided a detailed analysis of the scope and value of plantation forest as a renewable natural resource. Plantation forestry and forest products industries now have an increasingly important role in the national economies of numerous countries in the subtropics and tropics (Evans et al. 1993). Although most attention has been given to the task of managing native forests (e.g. Poore et al. 1989; Bruenig 1996), the successful management of plantations is also a significant challenge.

Despite often abundant solar radiation and in some regions high annual rainfall, there are many doubts about the long-term productive capacity of tropical plantations; the data for yields from them reflect this difficulty. Much of the land available for wood production has problems of low fertility, endemic seasonal drought or salinity. Tree plantations may be more tolerant of these conditions than alternative agricultural crops. They can provide useful yields while being more conducive to sustainable land use by virtue of reduced site disturbance, a capacity to conserve nutrients and in some cases fix atmospheric nitrogen, and sometimes to lower the level of high watertables and thus avoid the hazard of salinity. Although much of the early efforts to grow larger-scale plantations in the tropics concentrated on high-value species such as teak or mahogany, species of pines, eucalypts and acacias suited for industrial raw material or fuelwood are now used extensively. At the same time, there is considerable pressure to offer managers and landowners a greater choice of planting material, including indigenous species not previously cultivated.

In this chapter we set the scene for the subsequent chapters which form the core scientific, multidisciplinary analysis of plantation productivity. The world consumption of wood for industrial and domestic use is described. Demands on tropical forests are outlined. The extent, composition, yield and role of tropical forest plantations is considered. This account of the scope, extent and nature of tropical plantations provides a context for discussion of physical and biological factors relevant to the successful establishment and management of plantations to achieve high productivity in the long term.

The Global Demand for Wood

The demand for industrial wood (pulpwood, and saw and veneer logs) grew strongly between 1900 and 1950, but the rate of growth has declined since 1950 (Sedjo and Lyon 1990). In addition, there has been a shift away from solid wood products towards reconstituted and pulp products. Technological development has improved the efficiency of conversion and utilisation of roundwood: building codes have been revised to economise in wood use, trusses have reduced the amount of sawnwood needed to build a house; small young trees can be used to make plywood and other panel products with virtually no residue, decorative veneers can be peeled so thinly that one log can cover more than twice the surface previously possible, pressure-treated logs and timber last many times as long as untreated material exposed to decay and insect hazards, high-yield pulping processes can provide almost double the yield of paper that comes from the kraft process, light-weight coated papers take less pulp to make a page and used paper can be de-inked to make newsprint. Technological change beyond the industry will also influence the demand for forest products: the use of steel for house framing and the growth of electronic communications are examples. FAO (1993a) predicted industrial roundwood consumption to increase by 2.7% annually to 2674 million m^3 by 2010, but this figure may be too high (Aspey and Reid 1994, whose estimate is 1940 million m^3; Nilsson 1996); a recent FAO estimate (2278 million m^3 1995a) is more conservative. Consumption is related to price; real prices have risen and are expected to continue to do so (Aspey and Reid 1994). Consumption of wood products is closely related to Gross Domestic Product (GDP) and of course population. In developing countries, including those in the tropics, GDP and consumption per capita, as well as population, are rising. Despite the difficulty of accurately predicting the influence of technology on wood consumption and the demand for wood in a rapidly changing world, all estimates lead to a scenario of increased demand in the near future. Much of the demand will be for products which can be obtained from plantations.

Pulpwood

Pulp is an important end use of wood, in 1991 amounting to 653 million m^3 or 20% of total wood consumption. Total consumption in 1991 was 3.4 billion and by year 2010 may rise to 5 billion m^3 (FAO 1994). Around 1950, 95% of paper was made of wood fibre and 90% was from coniferous wood. Forty years later, with a five-fold increase in world consumption, wood fibre still accounts for 90% of total fibre input. The composition of the wood has changed; non-coniferous species now contribute nearly 30%, and an increasing fraction of this is made up of eucalypts, much grown in the subtropics and tropics (FAO 1994). Total paper consumption is expected to grow at about 4% per annum in the next decade. This will mean an increase in wood consumption over the period 1991–2010 of 60–80%, the lower figure reflecting a continued rapid increase in the extent of recycling paper so that virgin fibre will constitute only 50–60% of total fibre input. There is, however, little price incentive for increased paper recycling (Nilsson 1996). In developing countries, where most of the current production comes from plantations, the 1991 consumption of 60 million m^3 of pulpwood is expected to rise to 120 million m^3. To meet the projected demand for a further 60 million m^3 by 2010, the capacity of plantations to supply wood to industry will need to be doubled by that year, without which pressure on native forest will be even more severe. Increased supplies from plantations need not require a corresponding increase in area; better management of existing resources is a practical and important option in the medium term.

Saw and veneer logs

World production of sawn wood in 1991 was 457 million m^3, a figure expected to rise to 745 million m^3 by year 2010. The United States, Canada and the former USSR accounted for 231 million m^3. Annual consumption per capita in 1991 ranged from 0.612 m^3 in Canada to 0.080 m^3 in South America, 0.034 m^3 in Asia and 0.015 m^3 in Africa (FAO 1993a). The conversion of sawn volumes to roundwood equivalent entails making an estimate of the fraction of the log volume lost as residue in processing; the loss is of the order of 50%. Thus some 900 million m^3 of logs would be required for the total annual production cited above. Veneer production in 1991 was about 10 million m^3, of which about two-thirds was made in Asia.

Production of tropical saw and veneer logs in 1995 by member countries of the International Tropical Timber Organisation (ITTO) was 133 million m^3; the top five countries were Malaysia, Indonesia, Brazil, India and Papua-New Guinea (Johnson 1996). This corresponds to only about 15% of world sawlog production, and most of it is from native forest. Thus much of Africa and Asia contributes little to sawlog production, and consumes little compared with more affluent societies.

Plantations in temperate, developed countries are an important source of saw and veneer logs, but plantations in tropical countries do not promise large yields of these products. One reason for this is the emphasis on short rotations (and consequently small-diameter logs) in the tropics, due in part to the nature and importance of private-sector investment in those regions.

Fuelwood and charcoal

Although some use is made of these by industry (e.g. for smelting in Brazil) their largest use is as household fuels — in Africa, for example, about 90% of the population use fuelwood for cooking (Jepma 1995). There is a large global demand for fuelwood and charcoal: in 1991, 1830 million m^3 were used — 1595 million in developing countries — and it is anticipated that by 2010 demand will be 2395 million m^3 (FAO 1993a). In an earlier study, FAO (1981) concluded that the gap between potential demand and supplies of fuelwood likely to be available from a shrinking resource base will be about 960 million m^3 annually by the end of the 20th Century. In contrast, the anticipated deficit for industrial wood was small. In order to satisfy the projected demand for fuelwood in 15 surveyed countries, the then rate of plantation establishment would have required a ten-fold increase. There are doubts about the effectiveness of such an approach (Shepherd 1990). Fuelwood scarcity is most acute in arid and semi-arid areas with few industrial forests, and thus the provision of fuelwood and of industrial wood are separate management tasks. In some countries (e.g. Bangladesh, Pakistan, Philippines, Sri Lanka, Indonesia, Thailand), most fuelwood is derived from non-forest land — that is, land owned by consumers or their neighbours, or common land (Koopmans 1996). Although the fraction of fuelwood derived from forests may be less than previously expected, the 30% of supply obtained from that source in South and Southeast Asia represents a large volume of wood. In India the importance of firewood logs (as opposed to firewood twigs) has risen greatly in the last 15 yr. Although industrial roundwood production declined in some countries (e.g., in the Asia-Pacific region, in Bangladesh, Bhutan, Philippines, Sri Lanka and Thailand) over the 1983–1993 decade, fuelwood and charcoal production in the region grew everywhere at an annual rate of 1.4% or more (Bhattarai 1996). Nilsson (1996) summarised several studies, all of which projected significant growth in global 'demand' for fuelwood and charcoal, reaching levels of 2325 – 3800 million m^3 annually by 2010. Acute demand for fuel has several impacts; it promotes gathering of litter from forest and woodland sites and the complete removal of biomass at the time of harvest — sometimes including stumps — and thus often aggravates site decline through nutrient depletion, soil erosion and poor regeneration.

As fuelwood supplies from public land diminish, rural households are actively growing more of their own fuelwood— e.g. in Nepal (Amacher and Hyde 1993) and Malawi (Hyde and Seve 1993). Better understanding of the role of wood energy in national energy and forestry programs is emerging as a result of research, for example by the FAO Regional Wood Energy Development Programme in Asia.

Products from *Eucalyptus urophylla* plantations, grown on a rotation of 6–9 years in China.

Fuel stored under a straw thatch for domestic use.
(Photo: E.K.S. Nambiar)

Foliage is commonly harvested for eucalyptus oil, fuel or mulch.
(Photo: S.J. Midgley)

Stumps for fuel.
(Photo: E.K.S. Nambiar)

Poles for chip production in a small-scale operation.
(Photo: E.K.S. Nambiar)

Demands on Tropical Forests

The impact of population on forests is a consequence of the size of that population and the demand of each person for resources from the forest. The United Nations estimates (1991) predict that under a medium fertility scenario, global population will rise from 5.3 billion in 1990 to 10 billion by 2050 and then stabilise at 11.6 billion shortly after 2200. Avery (1995) contends that this projection is too high, and that population is likely to peak at about 8 billion in 2030 and then trend downwards. There is no doubt that population will increase in coming decades, especially in developing countries of the tropics and subtropics, and with it the demand for wood. Some subtropical and tropical countries are also increasing their share of the expanding global trade in wood products.

The type and amount of wood products consumed vary enormously between countries, and between urban and rural societies within countries. Consumption of industrial wood may closely reflect the standard of living, and may be an indicator of economic development. The annual per capita consumption of paper ranges from less than five kilograms in the poorest countries to tens of kilograms in the most advanced developing countries and over 100 kg in industrialised countries. Sawnwood consumption also varies in this way. Demand for wood and wood products has increased quickly in several developing countries whose economies are growing rapidly. Although demand for fuelwood may decline as economic growth and national energy policies allow progressive change from fuelwood to fossil fuel, the overall consequence of economic development is to put more pressure on forests to supply a greater and more diverse range of wood products.

Non-timber forest products represent a major part of the value of many native tropical forests (Panayotou and Ashton 1992). Single-species plantations typically are grown for timber, although there are opportunities to grow complementary species such as rattan, and the primary plantation species itself may yield tannin (Hillis 1989) or essential oil (Doran and Brophy 1990). In Malaysia, rubber plantations established for latex production have now become a valuable source of timber for furniture.

The most conspicuous demand made on forests, however, has been for the land on which they have grown. This land, mainly converted to agriculture, has contributed to the increased food production to feed a world population which has doubled in the past half-century. Average annual deforestation in the tropics during the 1980–90 decade was 15 million ha (FAO 1993b), reducing total pan-tropical forest cover to 1756 million ha in 1990. In addition to the forest lost to agriculture and urban use, additional area (about 6 million ha annually 1986–90) is logged and significantly disturbed (FAO 1993b). Despite campaigns and rhetoric to halt deforestation (FAO 1986; Anon. 1990) clearing of tropical forest to provide land for food production and domestic and industrial use continues. Within a relatively short time there will be a shortage of timber supply on a global scale, and rapid deforestation will continue unless arrested by firm policies (Jepma 1995).

Salient features of global wood production, and the significance of tropical forests in this, are evident in Table 1.1. The importance of industrial coniferous roundwood in developed and in non-tropical countries, and of fuelwood and charcoal in developing and tropical countries, is clear.

Table 1.1 Roundwood production in 1991 (million m^3) (FAO 1993a and ITTO 1993a). Figures in brackets are percentages of the column totals.

	Industrial roundwood, coniferous	Industrial roundwood, non-coniferous	Fuelwood and charcoal (mainly non-coniferous)	Total
Developed countries	948 (88)	263 (50)	235 (13)	1446 (42)
Developing countries	127 (12)	262 (50)	1594 (87)	1983 (58)
Total	1075 (100)	525 (100)	1829 (100)	3429 (100)
Tropical	118 (11)	156 (30)	1306 (71)	1580 (46)

Plantation Forests in the Tropics

Plantations of rubber, coffee, tea, coconut and oil palm are outstanding examples of tree domestication. Early examples of the establishment of plantations of forest trees in the tropics include teak (*Tectona grandis*) in India (1840), Burma (1856), Bangladesh (1871) and Indonesia (1871). Eucalypts were grown in Brazil for fuelwood and railway sleepers from 1910. In Africa experimental plantings before the first World War provided the basis for subsequent small operational programs. Preliminary introductions of exotics had been widespread before these dates (e.g. Zacharin 1978). Of the effort in the tropics, that in Indonesia was the most substantial, with the result that some 500 000 ha of plantations existed in that country in 1950, compared with 30 000 ha elsewhere in tropical Asia, 110 000 ha in tropical Africa and 40 000 ha in tropical America. Thus in the tropics by 1950 there were rather less than a million hectares of plantation as defined by FAO; by 1980 there were some 11.5 million and by 1990 almost 44 million (FAO 1995b), much more than anticipated (Lanly and Clement 1979). Some observers regard these figures with caution, citing ineffective establishment, confusion of replanting with new planting, and of planned with achieved planting, as possible inflationary factors. The many trees planted around houses, in woodlots and farms, and along roads and canals are difficult to include in an inventory, and in only some countries have they been included in the reported resources. FAO (1995b) has suggested that the reported 44 million ha represents about 31 million ha of effective plantation. Table 1.2 provides information about plantation areas on a country basis; annual planting rates in individual countries range up to 1.7 million ha in India in 1989–90.

Table 1.2 The area under plantations in the ten tropical countries which between them account for 90% of tropical plantations (FAO 1995b), excluding data for tropical regions of China[a].

Country	Total plantation area 1990 (million ha)
India	18.90
Indonesia	8.75
Brazil[b]	7.00
Vietnam	2.10
Thailand	0.76
Venezuela	0.36
Cuba	0.35
Bangladesh	0.33
Myanmar	0.33
Madagascar	0.31

[a] FAO (1993b) defines tropical countries as those in which more than 50% of the land area falls between the Tropics of Cancer and Capricorn, thereby excluding China from this table. The area of plantations in the three southern provinces of Guangxi, Guangdong and Hainan total 8.4 million ha, equivalent to 20% of the plantation area in China (Anon. 1994).

[b] For the same reason, all Brazilian plantations are recorded as tropical, but many are temperate.

A 14-year-old eucalypt plantation at Buriram, Thailand, which is providing sawlogs and a variety of poles and posts from thinnings. (Photo: A.G. Brown).

In addition, plantations of species not traditionally considered to be primarily for wood production are extensive and have become an important source of wood. The total area is about 14 million ha, mostly in tropical Asia. Rubber covers 7 million ha, coconut 4 million and oil palm 3 million (FAO 1993b).

The statistics presented above may be placed in a wider context by comparing them with data from some non-tropical countries (Table 1.3). This information is also subject to problems of inventory, and to the arbitrary assignment of countries to tropical or temperate zones or to development streams. For example, both China and Australia include land within the tropics, but have been excluded from the statistics for 'tropical' countries. The statistics nevertheless do provide a global perspective on the size and distribution of the plantation estate.

Table 1.3 Plantation areas in selected non-tropical countries in 1990 (FAO 1995b). The annual planting rates range up to about 1 million ha in China, USA and the former USSR.

Country	Total area (million ha)
Developed countries	
USA	31.85
Former USSR	23.80
Japan	10.67
Canada	5.02
New Zealand	1.24
Australia	0.96
Developing countries	
China	41.39[a]
Republic of Korea	2.00
Chile	1.45
South Africa	1.33
Argentina	0.80
Morocco	0.53
Uruguay	0.21

[a]Anon. 1994

Plantations: their place among ecosystems

Plantation development must take place within a holistic approach to land use and ecosystem management, rather than in isolation. While this philosophical view would be widely supported, we are well aware of the diverse and sometimes conflicting concepts, definitions, strategies and tactics that are endemic in its application (Chapter 15) (see e.g. Carrere and Lohmann 1996; Ferguson 1996). At an ecosystem level, forest estates and their management can be represented as a continuum in relation to conservation and production values (Fig. 1.1).

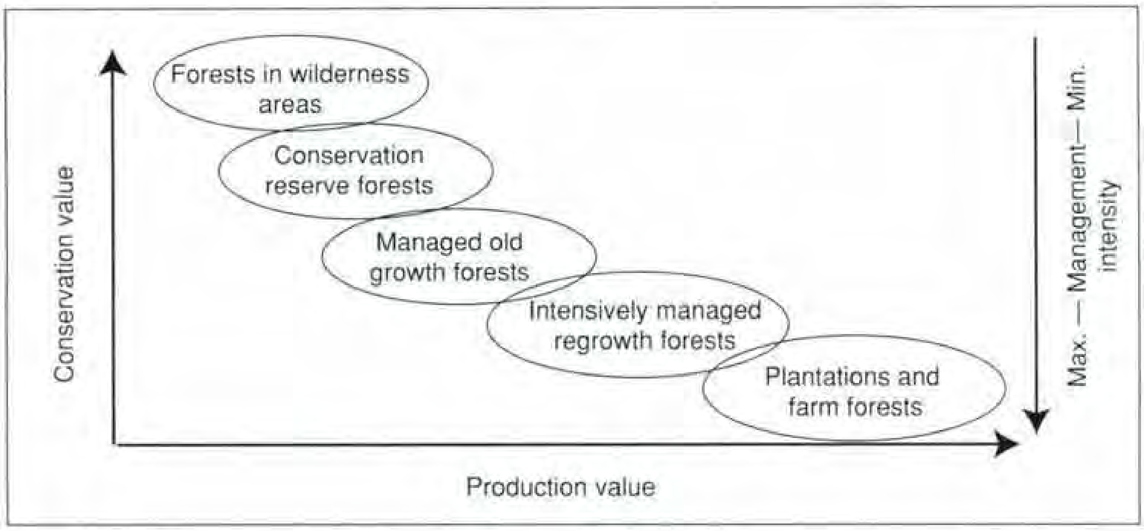


Figure 1.1 The production and conservation values of natural forests, plantations and agroforests may be represented as a continuum (adapted from Nambiar 1996).

It is important to think of different forms of land use as links in a continuum, and their interdependence in terms of ecosystems and sustained use. Each link provides multiple but not identical values. Plantations are an important link in this chain. The nature and extent of their overlap with other forests depends on factors including the choice of species (native or exotic; one or more) and the extent of genetic manipulation, and the intensity and nature of other management practices. A trend in managing planted forests in some States of the USA reflects a view that the structure and function of planted forests should closely resemble those of native forests.

Productivity of plantations at many sites is below the potential, and there are opportunities for increasing production on a wide scale by adopting appropriate soil and stand management practices. Factors which make the management of sustainable production in plantations distinctly different from that in native forests (Nambiar 1996) include:

1. Higher rates of production per unit area than in a native forest on a similar site, and thus more demands on the site;
2. Opportunity for planting at the start of every crop cycle superior genetic stock designed to grow better quality wood faster;
3. Greater incentives and opportunities for implementing intensive management techniques which ameliorate adverse effects of harvesting (e.g. ploughing and ripping to alleviate soil compaction, bedding to improve soil drainage, fertilizer application to replace nutrients) and control competition for site resources;
4. Management on 6–40-yr rotations, compared to 80–100-yr rotations in native forests, leads to more frequent and intense site disturbance;

5. Major opportunities to improve productivity (including wood quality) throughout the crop cycle by establishment practices, pruning, thinnings and fertilizer application;
6. Prospects of earlier returns from financial investment in market-oriented management; and
7. Opportunity for relatively less environmental conflict in production and harvesting wood.

No management can be applied to any form of land use (plantations being one) with 'no change' to the ecosystem. We should not resist changes which are necessary but know the risks and deal with them, and minimise or prevent impact on associated environments (see Chapter 15).

Choosing plantation species

Although only a small number of genera and species have been extensively used (Table 1.4), there is a widespread effort to expand the choice of species for plantations, and especially those established in the increasingly-important community forests. Boland (1989) and House and Harwood (1992) report a systematic effort to assess the value of a wide range of Australian species for cultivation in the tropics, an important outcome of which has been the identification of a number of acacias which succeed in arid tropical climates and produce large crops of edible seed. Other similar research is reported by Leakey and Newton (1993). These efforts have increased the range of nitrogen-fixing trees such as legumes and casuarinas which have a potential role in plantations, although knowledge of their biology and silviculture is rudimentary compared with that of many agricultural legumes.

Table 1.4 Distribution of areas of main plantation genera and species in the tropics in 1990 (million ha) (FAO 1993b).

Regions			**Genera and species**			**Total**
Tropical	**Eucalypts**	**Pines**	**Acacias**	**Teak**	**Others**	
Africa	0.79	0.61	0.25	0.145	1.2	3.0
America	4.07	2.78		0.015	1.77	8.6
Asia and Pacific	5.20	1.20	3.15	2.03	20.62	32.2
Total	10.06	4.59	3.40	2.19	23.59	43.8
	(23.00)	(10.50)	(7.70)	(5.00)	(53.80)	(100.0)

*Figures in brackets are the area of each species as a percentage of the total.

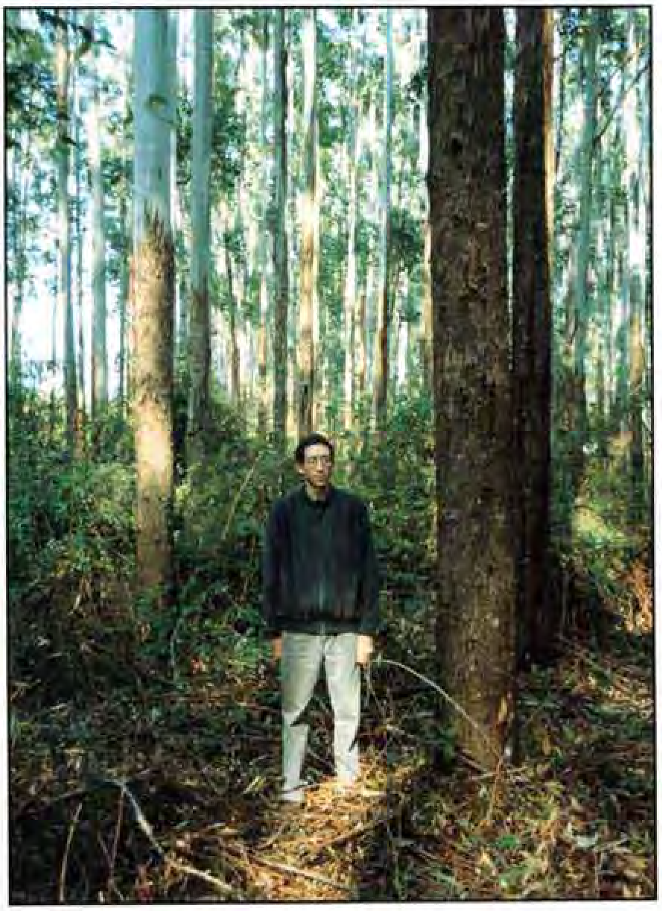
Examples of tropical forest plantations

The Jari project, just north of the Amazon River in Brazil, provides a case study of an endeavour to raise the productivity of a tropical forest plantation (Hornick et al. 1984). Over 100 000 ha of native forest were replaced with *Pinus caribaea*, *Gmelina arborea* and *Eucalyptus deglupta*. Hornick et al. (1984) and Whitmore (1992) have judged the project to be a success in terms of fibre production, a mixed blessing from the point of view of profit and a failure based on biodiversity values. The last conclusion was reached in relation to the original forest, but is unlikely to be true if the basis of comparison was pasture, a fate of large areas of tropical native forest. Eucalypt and pine plantations established elsewhere in Brazil on cleared agricultural land are valued as a national asset (Campinos 1991; Ondro et al. 1995).

The Malaysian Compensatory Plantation Project envisaged that about 100 000 ha would be established, commencing in 1982, using a 15-yr rotation with species such as *Acacia mangium*, *Gmelina arborea* and *Paraserianthes falcataria*. Ten years later, only 47 000 ha, mainly of *A. mangium*, had been planted (Thang 1992). Ng (1996) describes the series of difficulties the project experienced, culminating in the realisation that *A. mangium* is valuable for reclaiming degraded land and as a source of small-diameter timber, but that its potential for sawn timber has been misjudged.

Teak is indigenous to the Indonesian islands of Java and Muna, or became naturalised following introductions in 7th–14th Centuries. Almost all teak now in Java is in plantations established since 1895. Until 1969 it was the most important commercial timber (in volume and value) harvested in Indonesia, and it now forms more than half the production forest in Java where it occupies over one million ha. About a quarter of this plantation land is not well suited to the species. The principal silvicultural system used is clearcutting with tumpangsari (taungya), in which local people combine the growing of food crops and the tending of young plantation trees for 2–5 years during the regeneration period. The continuing success of the plantations is closely linked to participation by local people in their cultivation (Perum Perhutani 1993; Pratiwi and Lust 1994).

Thus the history of plantation development in the tropics reveals both successful outcomes and shortcomings, as is common with human endeavours. The success of plantation forestry in warm temperate areas (e.g. New Zealand, Chile, South Africa and Australia) does provide a basis for optimism regarding the development of plantations in the tropics, and the benefits which may be derived from them. Large-scale development of plantation forestry, especially on degraded lands, seems essential and inevitable in many tropical and subtropical countries.



Eucalyptus grandis, about 18 years old, Sao Paulo, Brazil. This stand has been thinned twice and is intended for sawlogs at about age 20 years. (Photo: E.K.S. Nambiar).

A mature plantation of teak (*Tectona grandis*) in Java (Photo: E.K.S. Nambiar)).

The species now used in plantations in temperate regions have been identified as a result of extensive testing over decades. Accounts of successes and failures were provided by Troup (1932), Streets (1962) and Poynton (1979), among others. Species for tropical sites are considered in more detail in Jacobs (1981), Turnbull (1986), Appanah and Weinland (1993), FAO (1995b) and Francis (1995). The extensive use of Australian species in other tropical countries is described by Brown (1993) and Vercoe (1993). Methods of integrating information on the climatic requirements and other site factors of species (based on their native habitat and sites in which they are cultivated) and matching this with the characteristics of potential plantation sites has made considerable progress in the last decade (e.g. Fig. 1.2). Such tools are already being used in a number of tropical countries embarking on plantation development. The end use of the plantation, with its allied socioeconomic questions, is critical in the choice of species and its management.

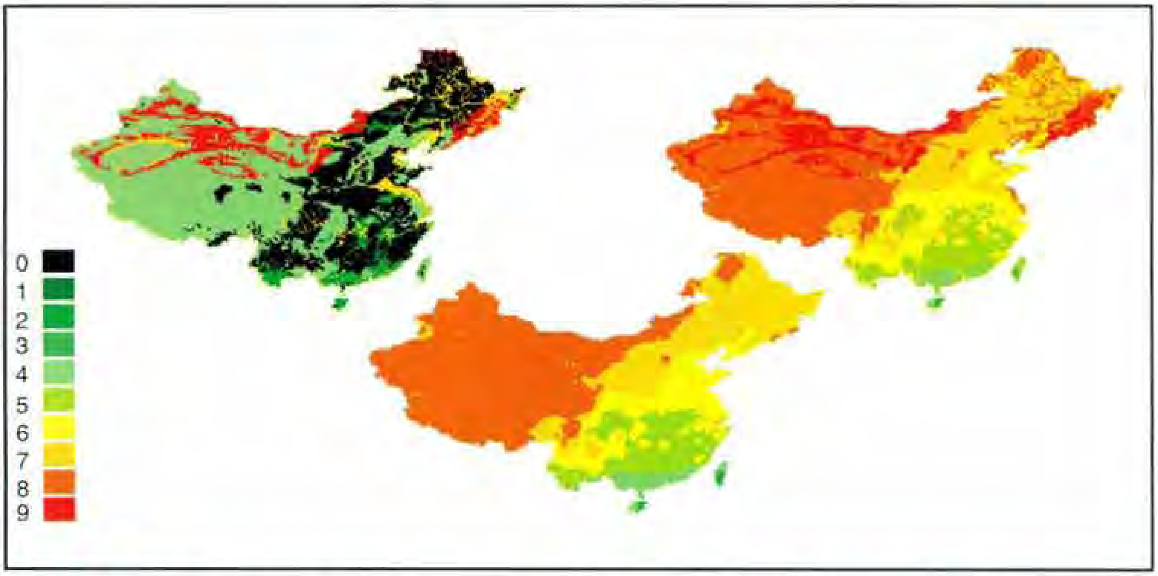


Figure 1.2 These maps illustrate the way in which climatic and soil information may be combined to indicate the suitability of potential planting sites for particular species and provenances; in this case the Petford provenance of *Eucalyptus camaldulensis* in China. The map on the left indicates the degree to which soil factors are expected to limit the growth of this provenance of the species. The colours indicate 10 degrees of limitation, ranging from black for no limitation (i.e. ideal conditions) to dark green for good conditions, through to yellow and orange for poor conditions and finally to red for most unsuitable. The map in the centre, in the same way, indicates how growth is expected to be limited by climatic factors. The map on the right combines information from the two other maps; the green areas having both soil and climate most suitable for this provenance (Booth 1996).

The very diversity of the tropical forest tree flora poses a challenge to plantation managers, and there is a strong temptation to use species which have succeeded elsewhere rather than to institute a search of the possibly extensive local flora. Widely-grown species typically have readily-available and easily-stored seed, need only simple propagation and inexpensive planting techniques, and have high survival and moderate to rapid growth in the field. Well-known species require no introduction to established markets. Rapid improvements in the genetic quality of planting stock of some widely-used species is progressively extending their superiority over unimproved (and perhaps little-known) populations of alternative species. This improvement has extended to wood quality (Zobel and Jett 1995) as well as to growth rate, stem form and disease resistance. The demand is increasing, however, for a more concerted effort to identify and domesticate 'indigenous' tropical species.

In some cases the contribution of plantations to landscape stability and amenity may become so great that it exceeds the value of timber production (Francis 1995). Similarly plantations can play an important role as a 'foster ecosystem' to regenerate vegetation on degraded tropical lands and enhance their biodiversity (e.g. Parrotta 1993).

Wood yield

The high potential yields of fast-growing species is frequently a factor in decisions to invest in plantations. Whereas the natural forest may have 'useful' increments of 1 or 2 m^3 of wood per year (Lanly 1982), plantations commonly produce about 10 m^3, in many cases 20–25 m^3 and in a few cases more than 50 m^3 (Evans et al. 1993). More examples of growth rates are given in Table 1.5.

Table 1.5 Productivity of main plantation genera in selected tropical countries (FAO 1995b)

Species	Region	Country	Rotation length (yr)	MAI (m^3 ha^{-1} yr^{-1})
Eucalypts	America	Brazil	8–10	18–20
	Africa	Burundi	8	1–2
		Congo	7	30
		Rwanda	8	8.5
		South Africa	8–10	18–20
Pines	America	Brazil	16–25	15–25
		Venezuela	10–20	10
		Chile	20–30	24
	Africa	Malawi	20–25	17
		Madagascar	15–18	6–10
		Mozambique	18–25	11
Teak	Asia	Bangladesh	60	2.6–3
		India	70	2.5
		Indonesia	50–70	1.25–2

Forecasts of yield and returns must be critically appraised when planning large-scale development. Factors that contribute to weakness in growth and yield predictions (Nilsson 1996) include poor knowledge of growth and yield; extrapolation of yield to a regional level from unrepresentative sites, over-zealous projection of gains from genetic improvement and biotechnology, and poor management caused by technical or socioeconomic factors. One common problem is the poor knowledge about the interaction between biophysical factors and productivity over the longterm and at regional scales (Chapter 15). Furthermore, there is increasing pressure on plantation forestry to be more 'environmentally accountable'. Although some such demands are motivated by 'environmentalism' (Carrere and Lohmann 1996), it is essential that plantations should be placed in the context of overall land use needs and in accord with environmental values.

These estimated national yields should be seen as merely indicative. A somewhat different data set was reported by Evans et al. (1993) for a number of species and environments. These data are therefore of limited value for comparison among countries because their basis is extremely variable. For example, ABCEL, an association of pulpwood producers in Brazil, estimated that the national yield level of eucalypt pulpwood plantations was 30 m^3 ha^{-1} yr^{-1} in 1980, steadily increasing to 42 m^3 ha^{-1} yr^{-1} in 1995 (see also Campinos 1991; Gonçalves et al. Chapter 11 and Chapter 15). Large differences in yield within species and genera are possible due to genetic and site effects. Differing mensurational procedures and quality may make comparison of reports difficult: bark volume is significant in young trees and its inclusion in increment figures results in their inflation; other sources of inconsistency are any definition of minimum log diameter and assumptions about stem form. The data nevertheless show that at a broad scale eucalypts are being managed on short rotations compared to pines, and that not all eucalypt plantations are 'fast growing'. It is also worth noting that extensive *Pinus radiata* plantations in temperate areas yield 20–35 m^3 ha^{-1} yr^{-1} over 25–35 yr rotations.

Factors relevant to productivity include:

- a large volume of standing timber in associated native forest may give a misleading impression of high site fertility;
- tropical plantations in their first rotation may have the benefit of nutrients and groundwater accumulated under the former cover;
- the geomorphology and properties of soil, and consequently soil-based constraints to production, may be poorly known;
- yields may be much lower than anticipated because of poor matching of species to specific sites, especially when seasonal drought and other constraints on available water are not recognised;
- the planting stock may be of poor genetic quality: sub-optimal provenance, inbred land race (e.g. Sim Boon Liang 1987) or a new collection from a natural stand;

- stocking may be low because of use of nursery stock of poor physiological quality, inadequate site preparation, ineffective weed control, damage from grazing and fire and illegal felling;
- undiagnosed and/or uncorrected nutrient deficiencies may be present; and
- planning, management and investment may be inadequate to achieve potential yields.

Through careful management it is possible to conserve site resources and at the same time obtain rapid growth of high-quality wood; conversely neglect of even one significant factor may doom the operation. Examples of well-managed plantations in the tropics are provided in Brazil by eucalypts (Campinos 1991; Ondro et al. 1995) and in Australia by *Araucaria cunninghamii* (Dale and Johnson 1991) and subtropical and tropical pines (Francis and Shea 1991).

The evolving role of plantation forests in the tropics

Several types of plantation development to suit particular land use objectives to advance economic and social well-being have been suggested (Evans et al. 1993).

The primary role of plantations is wood production, regardless of the size of the investment. The contribution of plantations to supplying the expanding world requirement for industrial wood has increased significantly over the years. The fraction of industrial wood produced from plantations, compared to natural forests, is presented in Table 1.6 for selected countries.

Table 1.6 Production of industrial wood from native forest and plantations (FAO 1995b)

Countries	Area (million ha)		Share represented by plantations (%)	
	Native forests	Plantations	Forest area	Wood production
New Zealand	7	1.20	16.1	93
Brazil	566	7.00	1.2	60
Chile	7	1.45	17.1	95
Argentina	34	0.78	2.2	60
Zimbabwe	32	0.07	0.2	50
Zambia	9	0.12	1.3	50
Australia	43	1.00	2.0	50

The striking observation in Table 1.6 is that although plantations represent only a very small proportion of the total forest cover in several countries, they have a large role in providing wood to those countries. This is because plantation forests are commonly more productive and readily managed than native forests in the same environment. Thus even forest-rich countries plan to increase the role of plantations in the production of industrial wood: in the case of Indonesia, from 20% now to 80% by the year 2030 (Indonesia/FAO 1990).

In the last ten years the importance and role of trees in rural development has become much more fully recognised by national governments and international agencies: growing trees which satisfy essential village needs (firewood, building and fencing materials, fodder, shelter and shade) is seen to be as important as industrial plantation development in most national plans of developing countries (Evans et al. 1993). Guidelines for plantation establishment and management have been developed (ITTO 1993b). The Consultative Group for International Agricultural Research (CGIAR), which is the hub of the international agricultural research centres, has extended the scope of its activities to focus attention on trees and forests through two organisations, the International Center for Research in Agroforestry (ICRAF) and the Center for International Forestry Research (CIFOR).

The potential of plantations to mitigate global warming by sequestering atmospheric carbon has been assessed (Dixon et al. 1991). While a significant quantity of carbon is accumulated in a growing plantation, the ultimate fate of the stemwood will determine how quickly the bulk of this is returned to the atmosphere.

Whereas initial rotations in temperate plantations may have lasted as long as 50 yr, those in some tropical plantations have been one-tenth as long, so that even after a couple of decades large portions of the tropical plantation estate may have been cropped several times, rapidly raising issues which have been addressed in less pressing circumstances in temperate environments. Plantations in the tropics seem to be poised for substantial expansion, and there is urgency to ensure that their management is soundly based.

Plantations in some warm temperate and tropical countries already provide raw material for industries which contribute significantly to national economies. Compared to most agricultural crops, the value added to wood by further processing, typically in a rural setting allied to the plantations themselves, is great. The aggregate effect may be to provide a higher level of employment and income for the plantation region than would be derived from alternative land uses. Experience from Brazil, Chile, New Zealand, South Africa and Australia (e.g. Dwyer Leslie Pty Ltd 1995) illustrates this.

The Challenge

Plantation forests will become increasingly significant in the tropics, and it is important that they be managed well from production, environmental, social and economic perspectives. The biophysical environment in the tropics is very diverse, yet some relevant factors are common—for example high solar radiation and high year-round temperatures, which are conducive to rapid growth if other factors are favourable. The great range in productivity which is encountered, however, suggests that ideal conditions are rare. Factors which are commonly most limiting are water availability and nutrient supply. The range of trees which might be grown is wide, reflecting the diversity of biophysical conditions under which the subtropical and tropical tree flora has evolved. The widespread environmental constraints on productivity, however, commonly lead planters to choose species from only a few genera which are tolerant of these conditions and are able to grow rapidly with additional inputs. There are good reasons to expand the range of genera and species from which managers may choose. While most of the examples used in this book are based on a few genera which are extensively used in plantations in both tropical and temperate regions, the principles illustrated are widely relevant. Prudent, informed managers can do much to minimise the environmental and economic costs of production, and research will continue to contribute to the balance between costs and benefits. It is important to understand that there will be no 'silver bullet' which at one stroke will resolve tensions between the need for increased production— be it at a village or industrial scale— and broader environmental impacts. The best overall strategy will depend on a comprehensive analysis of soil and physical considerations and the ecophysiology of the tree crop — discussed in detail in subsequent chapters — and adapting and delivering that knowledge as practical options and tools to growers. We repeat the plea to ensure that plantation development should be undertaken with due consideration of overall land use, and the social prosperity of societies in the local environment.

Just as research and its application has had a paramount role in the great increase in world food production which has enabled more people to be fed than ever before (Tribe 1994), research and the application of its results can do much to improve the outcome of plantation forestry. Historically most forest research effort has been directed at the temperate forests; it is now urgent to transfer as much relevant knowledge as possible from elsewhere to the tropics, and to identify and address the critical questions the resolution of which will contribute to successful sustained production from tropical plantations.

The purpose of this book is to bring together multi-disciplinary knowledge of soils, environment and eco-physiology in the context of the productivity of plantation forests. Emphasis is given to water and nutrients, two critical resources. Attention is drawn to management options that can be developed with current knowledge, and to issues about which further information is needed, to attain and sustain high productivity as a matter of priority.

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Genetic Resources for Plantation Forestry

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Abstract

Relatively few tropical tree species have been used extensively in plantations. Species of pines and eucalypts are used in about one third of the total area of tropical forest plantations, and acacias are also commonly planted. In utilising genetic resources effectively, it is important to assess the relative contributions of the genotype and the environment to the phenotype, and the relative magnitude of genetic variation at each level in the genetic hierarchy: species, provenances, and down to individual trees. The significance of quantitative variation and molecular genetics in the selection of genetic resources is discussed and the use of these different types of information in the design and implementation of tree improvement strategies described. Different approaches to the selection of genetic resources at each level of the genetic hierarchy are reviewed with particular reference to selection for water and nutrient use efficiency. While marker-aided selection, physiological testing and modelling may be valuable in the future, traditional field testing remains an absolute necessity.

FOREST PLANTATIONS are often established on land on which other forms of landuses have failed due to mismanagement or severe environmental constraints. Even on favourable sites, extremes of temperature, and especially of water availability, are usually faced by the newly planted seedlings. Limiting climatic factors, which are rather common for forest plantations, may be further exacerbated by low levels of organic matter and/or nutrients, or high levels of salinity or heavy metals. In addition to the problems posed by the environment of the planting site, the seedlings themselves are usually suffering some form of physiological stress due to transplanting from the nursery, and associated stresses resulting from transportation and storage. It is scarcely surprising, therefore, that so many tropical plantations fail (Bailly et al. 1982; Cossalter 1994). Various options exist to overcome the problems of plantation establishment, including site preparation and seedling acclimation. The correct choice of genetic material can be critical to early survival and longer-term productivity of plantations.

This chapter will describe the role that genetic resources can play in the successful establishment of plantations in the tropics. The current situation in the selection of genetic resources for tropical plantations is reviewed first. This is followed by a description of different types of genetic variation, and an outline of typical tree improvement strategies. The remainder of the chapter addresses the various approaches to selection of genetic resources for environmental stresses encountered in plantation establishment, using water stress as a specific example.

Genetic Resources in Tropical Plantation Forestry

Most forest ecosystems in the tropics are extremely rich in biological diversity. Those of the humid and sub-humid tropics are the source of important income through the harvest of timber. All forest formations of the tropics also provide a wide range of natural products useful to local populations. In spite of growing environmental concerns and the diminishing resource, wood and non-wood forest products are nowadays still largely harvested from natural forests. This situation is primarily due to economic reasons—although more restrictions are being placed on the harvest of natural forest products, their supply, in most cases, is still less expensive than if obtained from plantations. Long return-time on investment is a major constraint to tree planting.

Several other constraints also affect the domestication of tropical tree species. Basic knowledge needed to raise and propagate trees and carry out breeding programs is available for only a limited number of species. The large number of candidate species for domestication and the limited resources available for research make progress slow. Although the generation interval—the time needed to reach reproductive maturity and time elapsed before reliable selections can be made—is often less for tropical trees than for temperate ones, it remains a major reason why tree breeding is often viewed as a long-term investment.

About a third of the total area of forest plantations of the tropics is made up of eucalypts and pines (FAO 1993). With only a few exceptions, the most commonly planted species of these two genera originate from the seasonal humid and sub-humid tropics and subtropics. Some of the most important include *Eucalyptus camaldulensis, E. globulus, E. grandis, E. microtheca, E. tereticornis, E. urophylla, Pinus caribaea* var. *hondurensis, P. merkusii, P. kesiya, P. oocarpa* and *P. tecunumanii* (Evans 1992).The wide use of eucalypts and pines in the tropics is mainly related to the development of industrial plantations. Their fast growth, ability to adapt to new environments and short to medium rotation length are seen as definite advantages. Because of the spectacular success obtained with several eucalypts and pines when planted on suitable sites and properly managed, expectations are high. There is, however, a risk of misuse and off-site planting due to underestimation of their ecological requirements.

Many of the 800 species of acacias have a tropical distribution. They are found in very diverse environments ranging from equatorial humid to semi-arid conditions. Their ability to adapt to extreme conditions is reflected by their performance in plantations. *Acacia mangium* and *A. crassicarpa* are high-yielding when planted in moist equatorial regions; at the other extreme, *A. nilotica* ssp. *adstringens*, *A. tortilis* ssp. *raddiana* and *A. senegal* are among the most successful species on degraded lands of the semi-arid and arid zones (Souvannavong and Cossalter 1986).

In many instances, especially for producing pulpwood, there are few alternatives to eucalypts, pines or acacias, even though native fast-growing species may locally be available. Species of regional importance, such as *Anthocephalus cadamba*, *Endospermum malaccense*, *Endospermum peltatum*, *Octomeles sumatrana* and *Styrax tonkinensis* in Southeast Asia, *Chlorophora excelsa* in Africa and *Didymopanax morototoni* in the Amazonia region have been tested for pulp production, but are generally inferior to eucalypts, pines and acacias.

Several species are widely planted for the production of valuable timber or general utility timber in the tropics. These include *Cedrela odorata*, *Cordia alliodora*, *Cupressus lusitanica*, *Gmelina arborea*, *Paraserianthes falcataria*, *Swietenia macrophylla* and *Tectona grandis*. *Cunninghamia lanceolata* is also important in terms of extent of plantations, although mainly limited to southern China.

Multipurpose tree species (MPTs) are widely planted, especially for community or social forestry. In the Asia-Pacific region and Africa, MPTs represent 72% and 54%, respectively, of the total forest plantation area (FAO 1993). Latin America is the only region where large-scale plantations predominate with 59% of the total area (FAO 1993). MPTs are used mainly to meet local needs in areas which are short of wood and other forest products and, where land availability and markets permit, to supply forest products for artisans or small industry. The species planted by farmers vary considerably from one region to another. However, a few genera are of global importance. These include: *Acacia*, *Albizzia*, *Cassia*, *Casuarina*, *Cordia*, *Leucaena*, *Mimosa*, *Prosopis*, *Sesbania* and *Ziziphus*. In addition the following species are widely planted in all tropical regions: *Alnus acuminata*, *Azadirachta indica*, *Calliandra calothyrsus*, *Dalbergia sissoo*, *Gliricidia sepium*, *Grevillea robusta*, *Melia azedarach*, *Parkinsonia aculeata* and *Tamarindus indica* (Evans 1992).

Additional plantation species of regional importance which belong to genera not yet mentioned in this chapter can be found in each agroecological zone:

(i) Humid Africa: *Aucoumea klaineana*, *Khaya ivorensis*, *Khaya anthotheca*, *Khaya grandifoliola*, *Khaya senegalensis*, *Lophira alata*, *Maesopsis eminii*, *Nauclea diderichii*, *Pycnantus angolensis*, *Tarrietia utilis*, *Terminalia superba*, *Terminalia ivorensis*, *Thieghemella heckelii* and *Triplochiton scleroxylon* (Dupuy and Mille 1991);

(ii) Dry Africa: *Adansonia digitata*, *Borassus aethiopium*, *Euphorbia balsamifera*, *Leptadenia pyrotechnica* and *Parkia biglobosa* (Souvannavong and Cossalter 1986);

(iii) Asia–Pacific: *Agathis* sp., *Alstonia macrophylla*, *Anthocephalus cadamba*, *Araucaria cunninghamii*, *A. hunsteinii*, *Chukrassia tabularis*, *C. velutina*, *Dipterocarpus alatus*, *D. turbinatus*, *D. zeylanicus*, *Dryobalanops lanceolata*, *Duabanga moluccana*, *Hopea odorata*, *Lagerstroemia speciosa*, *Melaleuca leucadendron*, *Parashorea malaanonan*, *P. stellata*, *Pterocarpus indicus*, *P. macrocarpus*, *Samanea saman*, *Santalum album*, *Shorea johorensis*, *S. leprosula*, *S. multiflora*, *S. ovalis*, *S. parvifolia*, *Schleichera oleosa* and *Xylia dolabriformis* (Vivekanandan et al. 1992; Appanah and Weinland 1993);

(iv) Central America and the Caribean: *Bombacopsis quinata*, *Caesalpinia velutina*, *Erythrina berteroana*, *E. fusca*, *E. poeppigiana*, *Guazuma ulmifolia*, *Enterolobium cyclocarpum*, *Jacaranda mimosifolia*, *Swietenia humilis* and *Tabebuia rosea* (CATIE, various unpublished documents);

(v) South America: *Bagassa guianensis*, *Bertholletia excelsa* and *Didimopanax morototoni*.

Population improvement within species is well advanced for important industrial species such as *Araucaria cunninghamii*, *A. hunsteinii*, *Eucalyptus camaldulensis*, *E. globulus*, *E. grandis*, *E. tereticornis*, *E. urophylla*, *Pinus caribaea* var. *hondurensis*, *P. merkusii*, *P. kesiya*, *P. oocarpa*, *P. tecunumanii*, *Tectona grandis*, *Gmelina arborea*, *Cedrela odorata*, *Cordia alliodora*, *Cunninghamia lanceolata*, *Terminalia superba* and *T. ivorensis*. Examples of gain from these efforts include those for:

- *A. cunninghamii*, in which volume and straightness at 15 yr were improved by 38% and 68% respectively (Nikles et al. 1988; see also Nikles 1996);
- *P. caribaea* var. *hondurensis*, in which mean tree volume and a combined index of stem and branch quality were improved at 6 yr by more than 20% in each case (Nikles 1996);
- *Eucalyptus*, in which mean annual increments were increased from 28 to 45 m^3 $ha^{-1}yr^{-1}$ over 15 yr (Campinhos 1993).

Recently, tree improvement programs have been initiated in several regions for *Acacia mangium*, a species which dominates industrial planting in Southeast Asia, and *A. crassicarpa*.

Plantation and industry managers increasingly have more specific demands on the characteristics and quality of their products. Interspecific hybrids are sometimes better placed to fulfill these requirements than pure species. The most advanced breeding programs on interspecific hybrids are those involving *Eucalyptus grandis*, *E. pellita* and *E. urophylla* in Brazil and Congo, and *Pinus caribaea* var. *hondurensis*, *P. caribaea* var. *caribaea*, *P. elliottii* and *P. tecunumanii* in Australia (Nikles 1993a; see Nikles 1996 for examples of gains).

More than a thousand MPTs are cited as being used but only a relatively small number are included in breeding programmes. The tendency of farmers to produce their own planting stock in order to minimise expenditure may make it difficult to go further in population improvement with many seed-propagated MPTs. Examples of active breeding programs include those on *Acacia auriculiformis* and several other acacias from dry Australia and Africa, *Azadirachta indica*, *Calliandra calothyrsus*, *Dalbergia sisso*, *Faiderbia albida*, several *Leucaena* and *Prosopis* spp., *Tamarindus indica* and *Ziziphus mauritania*.

Genetics and Genetic Variation

Genes are the basis for all biodiversity. A major reason for the differences between ecosystems is the differences in their species composition. Similarly, differences among species are due to differences in their genes. Among individuals of a species there is also variability in genes which, however, is not so great as to preclude intermating.

Genes, being components of a macromolecule of DNA, are difficult to see and therefore difficult to manage.With modern technology, genes can be visualised through techniques such as isoenzyme analysis and various DNA analyses. The alternative approach is to observe the effects of genes. As genes act to determine the physiological and hence physical characteristics of organisms, observing the physiological or physical traits of organisms can provide information on their genes. A difficulty is that traits of great economic importance such as vigour involve complex physiological processes and a large number of genes. Furthermore, the external environment can also play a major role in determining the appearance (termed the 'phenotype') of individuals. Also, the genotype and environment often interact in such a way that the relative expression of genetic effects varies across environments. For all these reasons, measuring or even observing direct effects of genes and thus the 'contribution' of individual genes in trait expression is not possible in most cases.

To overcome this difficulty geneticists have developed a simplified model of gene action where the relationship between phenotype, genotype, and environment is simply stated as:

$P = G + E + G \times E$

where:

P = phenotype,

G = genotype,

E = environment, and

G × E = genotype–environment interaction.

This equation is the basis for all quantitative genetics, and is also of utmost importance in tree breeding strategies.

Genetic diversity is organised in a hierarchical fashion; four levels of variation are usually recognised: the species, provenance, family and individual levels. All species, even when relatively closely related such as some eucalypts, represent a distinctive combination of characteristics for adaptation, habit, form, vigour, wood properties, etc. Species variation is relatively easy to recognise in nature and to exploit in tree breeding, although in many cases the reproductive barriers may not be clear-cut, resulting in taxonomic uncertainty over the status of some species. Species which can exchange (even to a very improbable extent) genes through natural or controlled mating events belong to a complex of such species, among which hybridisation is possible.

At lower levels in the hierarchy, the emergence and maintenance of more or less marked genetic variation is a consequence of an accumulation and combination of factors which over time have prevented panmixy (i.e., completely random mating among all individuals). In some cases the present distribution and differentiation of certain populations can be explained by migration and isolation processes induced by events of past geological eras, especially changes in climate and sea level. Nowadays, genetic forces resulting from human activities, for example random drift following habitat fragmentation or natural selection on degraded sites, lead to greater genetic differentiation. The mating system (outcrossed or inbred), mode of dispersal of seed and pollen, and population size are important in determining the degree of genetic differentiation within species.

Quantitative genetics

The traditional approach to determining genetic variation is through the assessment of quantitative (measurable, continuously variable) traits or qualitative traits. Study of the genetic variation in quantitative traits aims to: i) identify individuals carrying interesting genes or gene combinations; and ii) forecast the genetic gain which can be achieved in each new generation by crossing selected individuals. Quantitative genetics primarily deals with the transfer over generations of quantitative traits at the population level. It makes use of the hierarchical nature of genetic variation and the additive nature of variances to estimate the proportion of phenotypic variation that can be attributed to genetic effects. This proportion is most often expressed in terms of the *heritability* of a trait (h^2). A good discussion of the various types of heritabilities and their estimation is provided by Namkoong et al. (1966). It is important to recognise that heritability is a variable that changes with environment, genetic material and age. This is demonstrated in Tables 2.1, 2.2, 2.3 and 2.4. In addition to the variability in heritability estimates evident from these tables, it is clear that heritability for traits of particular interest to the tree breeder such as height, diameter, volume and stem straightness often has low value, indicating the relatively strong role of the environment in determining phenotype. It can be seen that family heritability is larger than individual tree heritability.

The gain from selection depends on the intensity of selection, the total amount of variance and how much of the variance is heritable. Not all the genetic variance is available for selection and transmission; the part which is available is called 'additive'. The part which is not available is due to non-additive effects such as dominance.

The formula for calculating genetic gain (ΔG) is:

$\Delta G = h^2 \, . \, i \, . \, \sigma_p$

where:

i = the selection intensity, and

σ_p= the phenotypic standard deviation.

This strictly applies only to mass selection without reference to pedigree. Typical values for the three terms in this equation differ for selection among individual trees (mass selection) and selection among families, that is when using pedigree information. The selection intensity (and the phenotypic standard deviation) is usually higher among individual trees, while heritability is usually higher at the family level.

Genetic gain in chosen traits is achieved at every stage of the 'benefit capture' component of a breeding program (see below). Typical ways in which genetic gain is captured are through mass selection, in which individuals are selected on the basis of their phenotype; through family selection; and through clonal selection or, as in most breeding programs, a combination of the above. While in general the magnitude of gain increases with sophistication of the selection process (Table 2.5), gains are additive and most breeding programs will capture the most easily exploited gains first, e.g. through simple mass selection. Most tree breeding programs focus on a few economically-important traits, e.g. growth rate, stem form, crown quality and wood quality. Concurrent improvement in multiple traits is possible if the genetic correlations between traits is favourable, but this is not always the case (e.g. Dieters 1996).

Table 2.1 Estimates of individual tree and family heritabilities for two species of tropical pine growing in Congo, Zimbabwe and Queensland (adapted from Crockford et al. 1989 and Kanowski and Nikles 1989)

Species and location	No. of provenances	Height		Diameter		Stem volume		Stem straightness	Wind firmness
		h^2_i	h^2_f	h^2_i	h^2_f	h^2_i	h^2_f	h^2_i	h^2_i
Pinus oocarpa									
Congo	4	0.16–0.63	0.35–0.74	0.01–0.35	0.04–0.57				
Zimbabwe	8	0.06–0.54	0.33–0.83	0.12–0.52	0.49–0.87	0.11–0.38	0.50–0.80		
P. caribaea var. *hondurensis*									
Zimbabwe	8	0.04–0.54	0.25–0.85	0.08–0.67	0.39–0.88				
Queensland	4	0.20		0.30				0.24	0.08

Table 2.2 Estimates of family heritabilities for two species of tropical eucalypts (Eldridge et al. 1993; Wei and Borralho 1995)

Species	Age (yr)	Height h^2_f	Diameter h^2_f
Eucalyptus tereticornis	4	0.16	0.11
E. urophylla	1	0.25	0.19
E. urophylla	2	0.27	0.18
E. urophylla	3	0.37	0.25
E. urophylla	4	0.39	0.34

Table 2.3 Clonal (i.e. broad-sense) and family heritabilities for selected trees (selection intensity 1:2000) and random trees of *Eucalyptus grandis*, growing in Brazil (Kageyama and Kikuti 1989)

Character	Selected trees		Random trees	
	h^2_{clone}	h^2_f	h^2_{clone}	h^2_f
Height	0.27	0.28	0.08	0.28
Diameter	0.22	0.26	0.29	0.22
Stem volume	0.29	0.36	0.32	0.26

Table 2.4 Family heritabilities (h^2_f) for open-pollinated and control-pollinated families of *Eucalyptus grandis* growing in South Africa (Van Wyk 1976; Malan 1988)

Character	Age (yr)	Open-pollinated h^2_f	Control-pollinated h^2_f
Height	5	0.39	
	1		0.11
	8		0.45
Diameter	5	0.39	
	8		0.30
Volume	6	0.19	
	1		0.10
	8		0.53
Crown form	8		0.33
Stem form	8		0.46
Wood density	8		0.45
Fibre length	8		0.54

Molecular markers

Given the confounding effect of the environment in observing the effects of genes, it might be assumed that techniques offering ways to directly visualise genes without the complication of environmental effects have valuable potential in the understanding and control of genetic variation. Indeed, in recent decades, there have been innumerable studies on genetic variation in plants and animals using isoenzyme analysis, and more recently various types of DNA analyses, such as restriction fragment-length polymorphisms (RFLPs), randomly amplified polymorphic DNA (RAPDs) and short sequence repeats (SSRs, or microsatellites). Most of these molecular markers are not affected by environmental effects, so the observed phenotype is a direct reflection of the genotype. Also, many markers are co-dominant, allowing heterozygotes to be distinguished from homozygotes.

Such studies have provided information on a number of important issues related to both conservation of genetic diversity and its utilisation for plantation establishment. We have learnt that, in general, forest tree species are highly heterozygous, i.e. contain high levels of genetic variation, tend to be highly outcrossed, and contain a high proportion of the total genetic variation within populations or provenances (Table 2.6). Loveless (1992) summarised much of the available information from molecular marker studies of tropical tree species. She demonstrated that tropical cultivars, mainly fruit species, have higher levels of polymorphism and heterozygosity than native woody taxa. Among tropical forest tree species, early successional species, which are most commonly used in commercial plantations, tend to have lower levels of polymorphism and heterozygosity than late successional species, though the average population differentiation is similar. The potential for molecular marker-aided selection exists but, as discussed below, there are a number of practical and theoretical problems for such an approach for forest trees.

Comparison of information from molecular markers and quantitative genetics

The two approaches to studying genetic diversity described above are clearly very different. Molecular markers offer a quick, easy and cheap method that is generally free from confounding environmental effects. However, the traits being studied are either enzymes or DNA sequences, which are at best only remotely related to the adaptive traits that are significant for tree growth in plantations. Therefore, for molecular markers to be useful in tree breeding and selection, there must be some relationship between patterns of variation for molecular markers, and patterns of quantitative variation.

The evidence for correlation between patterns of variation in molecular and quantitative traits is equivocal. One of the most comprehensive studies on this topic was conducted by Furnier et al. (1991) on white spruce (*Picea glauca* (Moench) Voss). These authors studied variation in 9- and 19-yr height growth and at six allozyme loci for 22 seed sources from across the range of white spruce in North America. Although there were strong longitudinal and latitudinal trends in height growth, no geographic trends were observed in the allozyme data. They interpreted this to reflect the different evolutionary forces acting on the genes responsible for the different types of genetic variation. Specifically, they proposed that allozyme loci may be selectively neutral, or near-neutral, and that therefore low levels of gene flow are sufficient to overcome the effects of other genetic forces. In contrast, as adaptive traits are under strong selection, the effects of low levels of gene flow are obscured.

In contrast, Liengsiri et al. (1995), studying allozyme variation in 11 populations of the leguminous *Pterocarpus macrocarpus* in Thailand, found a marked trend with longitude. This corresponded to the pattern of rainfall in central and northeastern Thailand, and also parallels preliminary evidence for geographic variation in early height growth of the species (Whuangplong et al. 1994). Soonhuae et al. (1994) similarly found marked differentiation between central and northeastern populations of another legume, *Dalbergia cochinchinensis* Pierre, matching the pattern of variation in height growth. Allozyme variation for various Australian species has also been shown to have geographic pattern corresponding with variation in morphological characters or growth rates (Moran 1992; Khasa Phambu 1993).

Although geographically similar patterns may exist, allozyme data cannot currently be used to predict growth responses. Whilst it is not currently possible to

Table 2.5 Relative genetic gains expected for *Eucalyptus globulus* for various improvement options in Australia (from Griffin 1994)

Option	Additional gain cf. option 1 (%)	Lead time (first yr of planting stock availability)	Indicative net benefit of gain (volume only) ($/ha)
1. Unimproved seed	0	1	
2. Culled seedling seed orchard	7.5	6	227
3. Culled clonal orchard	14.4	8	402
4. Mass propagated control-pollinated families of outstanding parents	22.5	9	556
5. Tested clones from control-pollinated families	25.7	13	484

Table 2.6 Typical levels of heterozygosity, outcrossing rates and F_{ST}/G_{ST} for tropical tree species. The figures for F_{ST}/G_{ST} indicate the proportion of total genetic diversity that is due to differences among populations

Species	Heterozygosity	Outcrossing rate	F_{ST}/G_{ST}	Reference
Acacia auriculiformis	0.146	0.925	0.182	Moran et al. (1989b)
	0.122	0.959	0.181	Khasa Phambu (1993)
	0.081		0.270	Wickneswari and Norwati (1991)
A. crassicarpa	0.141	0.960	0.093	Moran et al. (1989b)
A. mangium	0.017			Moran et al. (1989a)
	0.064		0.086	Khasa Phambu (1993)
Agathis boreensis	0.122			Kitamura & Mohamad-Yusof (1992)
Alseis blackiana	0.374		0.048	Hamrick and Loveless (1989)
Beilschmiedia pendula		0.918		Hamrick and Murawski (1990)
Bertholletia excelsa		0.850		O'Malley et al. (1988)
Brosimum alicastrum	0.225	0.876	0.055	Hamrick and Loveless (1989)
Carapa guaianensis	0.120		0.046	Hall et al. (1994)
Casuarina cunninghamiana	0.211		0.264	Moran et al. (1989c)

Table 2.6 (cont'd) Typical levels of heterozygosity, outcrossing rates and F_{ST}/G_{ST} for tropical tree species. The figures for F_{ST}/G_{ST} indicate the proportion of total genetic diversity that is due to differences among populations

Species	**Heterozygosity**	**Outcrossing rate**	**F_{ST}/G_{ST}**	**Reference**
Cavanillesia platanifolia		0.458		Murawski et al. (1990)
Cecropia insignis	0.146			Hamrick and Loveless (1989)
Ceiba pentandra		0.689		Murawski and Hamrick (1992)
Dalbergia cochinchinensis	0.229	0.993	0.127	Soonhuae et al. (1994)
Dipterix panamensis	0.162			Hamrick and Loveless (1989)
Dryobalanops aromatica	0.270	0.926		Wickneswari (pers. comm.)
Erythrina costaricensis	0.205		0.046	Hamrick and Loveless (1989)
Eucalyptus cloeziana	0.205		0.110	Turnbull (1980)
E. grandis	0.167		0.120	Moran and Bell (1983)
Gustavia superba	0.222		0.022	Hamrick and Loveless (1989)
Neobalanocarpus heimii	0.390	0.950		Wickneswari (pers. comm.)
Pinus caribaea	0.212			Ledig (1986)
P. caribaea var. *bahamensis*		0.890		Matheson et al. (1989)
P. caribaea var. *hondurensis*		0.910		Matheson et al. (1989)
P. kesiya	0.169	0.825	0.039	Boyle et al. (1991a, b)
P. maximinoi		0.650		Matheson et al. (1989)
P. merkusii			0.041	Changtragoon and Finkeldey (1995)
P. oocarpa	0.183			Ledig (1986)
		0.885		Matheson et al. (1989)
Pithecellobium pedicilare		0.951		O'Malley and Bawa (1987)
Platypodium elegans	0.251	0.921	0.073	Hamrick and Loveless (1989)

Table 2.6 (cont'd) Typical levels of heterozygosity, outcrossing rates and F_{ST}/G_{ST} for tropical tree species. The figures for F_{ST}/G_{ST} indicate the proportion of total genetic diversity that is due to differences among populations

Species	Heterozygosity	Outcrossing rate	F_{ST}/G_{ST}	Reference
Poulsenia armata	0.250		0.052	Hamrick and Loveless (1989)
Psychotria faxlucens	0.495	0.792		Perez-Nasser et al. (1993)
Pterocarpus macrocarpus	0.246		0.121	Liengsiri et al. (1995)
Quararibea asterolepis	0.256	1.008	0.022	Hamrick and Loveless (1989)
Shorea laevis	0.182	1.498		Wickneswari (pers. comm.)
S. megistophylla		0.737		Murawski et al. (1994)
Sorocea affinis	0.239		0.053	Hamrick and Loveless (1989)
Stemonoporus oblongifolius	0.342	0.840	0.163	Murawski and Bawa (1994)
Swatzia simplex var. *ochnacea*	0.272		0.055	Hamrick and Loveless (1989)
Tachigalia versicolor	0.073	0.937	0.070	Hamrick and Loveless (1989)
Tectona grandis	0.386	0.983	0.087	Kertadikara (1992)
Trichilia tuberculata		1.077		Hamrick and Murawski (1990)

utilise information from molecular markers directly in making decisions on tree improvement strategies (see further discussion on marker-aided selection, below), allozyme and DNA data can provide useful supporting information. For example, the magnitude of genetic variation can be usefully detected by molecular markers, and information on mating systems derived in this way can be especially valuable for the advanced stages of a breeding strategy.

Tree Improvement Strategies

Tree improvement aims at producing, for a given site, the planting material which displays the best results in terms of quality, productivity and adaptation (including resistance to insects, disease and climate), so as to satisfy given economic requirements. Selection and breeding may also be aimed at producing plantations that satisfy specific ecological or sociological needs, such as dune stabilisation and reforestation of arid or saline soils, or various kind of degraded lands.

Although tree improvement methods are based on rather complex techniques and often require complicated calculations, the approach of the tree breeder remains fairly pragmatic. The first step is to make maximum use of the existing natural variation. This implies that exploration and sampling of populations and individuals will be carried out throughout the entire natural range of the species considered for genetic improvement. Subsequently this material will be screened in different evaluation trials which will better assess the extent of the natural variability and will lead to selection of the populations, families and individuals which possess the genetic traits required (vigour, plasticity, disease resistance, good stem form, desirable wood quality, etc.). A basic tree improvement program is depicted in Figure 2.1. Though the details vary widely, the two components of breeding and benefit capture are common to all breeding programs.

At a more advanced stage of breeding, new genetic variation is created through recombination of variation existing in a selected or 'breeding' population. There are several degrees of control of the mating process. These range from some control of the average quality of the female and male parents, where the reproduction is through open pollination, to full control of both parents in the case of controlled crossing involving pairs of previously evaluated individuals. In recent years, non-sexual methods of recombining genetic variation have been developed. These include genetic engineering, mutagenesis, induction and selection of somatic variation and somatic fusion (Haines 1994; Griffin 1996).

Breeding and propagation strategies

Key components of tree improvement are breeding and propagation strategies. Their formulation requires an understanding of variation, genetic gain and methods

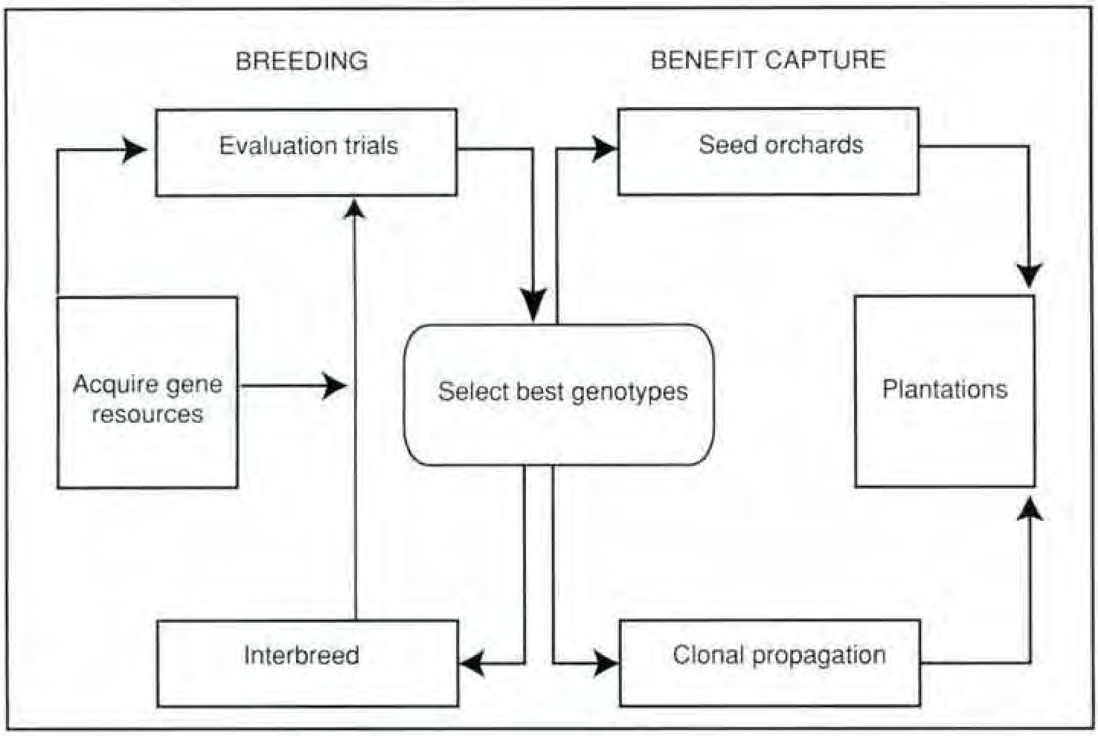

Figure 2.1 The principal elements of a conventional tree breeding program

of realising genetic gain (Nikles 1993b). The aim of a breeding strategy is to produce, each generation, improved (in terms of yield, quality and adaptation) base and breeding populations, while maintaining diversity. Various breeding strategies (single and multiple populations) are used in tree breeding programs; each has different consequences on population structure and the delivery of genetic gain. The aim of a propagation strategy is to ensure rapid and effective transfer of gains achieved in the breeding populations to the operational planting stock.

Breeding and propagation strategies should be well-integrated (Shelbourne 1991; Mullin and Park 1992; Mullin et al. 1992). In the case of commercial forestry such strategies should bring adequate economic returns. Researchers such as Namkoong et al. (1966), Cotterill (1986), Cotterill and Jackson (1989) and Shelbourne (1991) have made important contributions to the development of the concept of genetic gain per unit time and cost. Examples of strategies and plans for eucalypts are given by Eldridge et al. (1993). An explicit strategy is important, even when the scale of the work is small, as it ensures that there is an enduring framework which bridges changes in staff and integrates dispersed activities. Further work is still needed for more accurate evaluation of alternative breeding and propagation strategies (in terms of genetic gain, resource use and maintenance of genetic diversity) over time, for both industrial and non-industrial species.

Exploration, sampling and seed collection

The first step in evaluating the genetic potential of a species is to explore and sample populations and individuals from the range of natural distribution. There are relatively few examples of intensive range-wide exploration, sampling and seed collection for tree species. Exploration and sampling are often done on an ad hoc basis to satisfy the most immediate need for genetic material.

In the absence of information on the genetic variability within the species under consideration, it is difficult to decide what part of the natural distribution should be given priority for exploration and sampling and afterwards which provenances to test in species and provenance trials. Despite the increasing number of isozyme studies on tree species (Table 2.6), for most species basic information on genetic variation is lacking.

A common approach for guiding exploration and sampling when there is no information on the structure of genetic diversity within a given species is to sample according to the diversity of habitats. For species that respond to known environmental variables, including the co-evolution of other species, sampling from the range of those variables is an efficient method for capturing significant genetic variability (Namkoong 1986). Sampling should also extend to areas having ecological conditions which are marginal in comparison to those of the proposed area of utilisation. Such outlying populations might contain genes (possibly lacking in the 'core area') that might prove useful subsequently in improving environmental adaptability, disease resistance or quality.

Species and provenance evaluation and selection

The largest, cheapest and fastest gains are to be made by ensuring that plantations are established using the best available species and seed sources within species (Zobel and Talbert 1984). Table 2.7 shows an example of the importance of correct choice of species and provenance, and also emphasises the existence of species × site interaction. On site 1, the PNG provenance of *Acacia mangium* yielded a 60% improvement in height growth over locally-produced *Acacia auriculiformis*. On site 2, however, a PNG provenance of *A. auriculiformis* was best, and yielded a 45% improvement in height growth over locally-produced *A. mangium*.

Species evaluation and selection generally proceeds through several stages. The sequence described by Burley and Wood (1976) consists of three consecutive phases. The species elimination phase is the mass screening of a large number of possible species in small plots for a short period (0.1–0.2 rotation) to determine survival and promise of reasonable growth. The species testing phase is assigned for the critical testing or comparison of a reduced number of promising species in larger plots for longer periods (0.25–0.5 rotation). The species proving phase is designed to confirm, under normal conditions, the superiority of a few probable species.

In practice less thorough approaches are often adopted due to time constraints. It is important, however, that a species is adequately represented in early trial introductions to new sites. There is ample evidence from such trials conducted over the last two decades of a species having been 'eliminated' in early trials, only to be reinstated as one of the best later, when the species range was more widely or intensively sampled (Davidson 1992). Therefore, in species elimination and species comparison trials, at least three seed sources may be required: one from the area of optimum growth, one that is the closest climatic match and one marginal source from the boundary of the distribution that extends the range in the desired direction, e.g. towards tolerance of a lengthy dry season in a monsoon climate (Edwards and Howell 1962 in Davidson 1988).

Table 2.7 Performance at 4 yr of age of *Acacia auriculiformis* and *A. mangium* provenances on two sites in Sabah, Malaysia (Evans 1992)

Species	Provenance	Height (m)	
		Site 1	Site 2
Acacia auriculiformis	Sepilok (local)	9.87	11.51
A. auriculiformis	Balamuk,PNG	12.10	13.99
A. auriculiformis	Iokwa, PNG	14.91	13.07
A. auriculiformis	Bula, PNG	11.59	12.27
Acacia mangium	Tawau (local)	11.48	9.56
A. mangium	PNG	15.61	13.04

Provenance evaluation generally proves particularly rewarding as it is the step which provides the highest expectation of gain by unit of time. Also, potential gains are enduring and findings can be put to immediate use (there need be no delay between obtaining the evaluation results and the direct use, on a large scale, of seeds from provenances identified as the best adapted and highest performing ones). Provenance evaluation and selection are carried out through provenance trials; an example of a trial in which major differences were evident is shown in the photo at the top of page 42.

Despite these substantial benefits to be obtained from species and provenance selection, there are also dangers. Care must be taken, especially with exotic species, that the species and provenance samples are representative and have an adequate genetic base, otherwise the initial encouraging results will be short-lived. An excellent example of this comes from the introduction of *Acacia mangium* into Sabah, Malaysia. The initial introduction consisted of open-pollinated progeny from a single parent. Subsequent generations of inbreeding and selection within this

Variation between provenances of *Acacia aulacocarpa* in a trial at Chantaburi, Thailand planted in 1985 and photographed in 1989. The seed of the plot on the left was from Keru, PNG, while that of the plot on the right is from from Garioch, Queensland. (Photo K. Pinyopusarerk).

Established landraces of exotic species may perform much more poorly than newly-introduced but unimproved provenances. In this trial at Kanzenze, Rwanda the *Eucalyptus camaldulensis* on the left was grown from seed from Petford, Queensland, while seed for the tree on the right was gathered from the local landrace in Rwanda. (Photo A. Kalinganire 1987).

single family caused dramatic reductions in yield (Griffin 1990). Such histories are often one reason why performance of widely-used landraces of exotic species may be much below the potential of the species (see photo at the bottom of page 42).

Selection and breeding

Selection and breeding are critically important activities of a tree improvement program. Three stages are involved in this process:

i) Obtaining information on genetic parameters which enables the breeder to judge the potential of selection and to determine the best methods;

ii) Identifying potentially useful genotypes with desirable genes or gene combinations and;

iii) Cross-pollination of the selected genotypes so as to increase the frequency of desirable genes or gene combinations in subsequent generations.

These three stages are collectively called a selection cycle. Activities in the cycle are mainly concerned with formulation of mating designs, evaluation of resultant progeny and selection of desirable genotypes for propagation and further breeding for the next generation.

A wide variety of mating designs is available for assessing the breeding value of selected parents. In breeding half-sib families the alternative is either open pollination or polycross (the latter offers more possibilities of control of the pollen parentage). Mating designs for full-sib families range from complete or incomplete diallels to single pair mating and factorial designs. All such designs are costly, so the breeder needs to choose a design that is the most precise and cost effective for the purpose. Genetic information derived from the progeny of such mating designs includes specific and general combining abilities and their variances, reciprocal and maternal effects, narrow and broad-sense heritabilities of each trait, genetic and environmental correlations between all pairs of traits, and genotype-environment interaction effects (Burley and Barnes 1988).

Progeny evaluation

Moving from provenance evaluation to family/genotype evaluation increases in most cases the complexity of selecting appropriate sites and experimental designs and undertaking trial analysis. A first source of difficulty is the large number of treatments that, almost unavoidably, progeny trials contain. For trials with large numbers of treatments it is often not possible to find homogeneous areas large enough to contain complete replications (blocks). A second source of difficulty is the rather low heritability of most of the economically-important traits such as growth rate.

The risk with progeny trials is that environmental variance obscures genetic variation unless environmental variation within the trial site is minimised. Incomplete block designs (i.e. in which each block contains only some of the treatments) can alleviate this difficulty to some extent and, in reducing within-block variation, increase the precision of comparisons among treatments (Williams and Matheson 1994). It is important that progeny trials receive intensive silvicultural care, especially in ground preparation and post-planting maintenance, in order not to exacerbate site heterogeneity with uneven regrowth of grass and scrub vegetation.

Success in a tree improvement program depends on the accuracy of selection of genetic resources. With trees, expression of important traits may require several years when a mature phase of development is reached (time to age-stable performance). Performance of genotypes at young ages is imperfectly related to that at maturity. The quandary presented in tree improvement programs is that the increased genetic gain from early selection is at the expense of absolute genetic gain per generation (Cheliak and Rogers 1990). More research is needed on age-age correlation to determine how early we can select on different traits. In the present state of knowledge, any search for maximum accuracy in selection imposes a requirement to deal with mature trees. A number of approaches are possible, and these are discussed in detail below.

Seed production stands and plantations

Until some ten yr ago mass production of improved material of tropical trees was predominantly from open pollination between selected individuals, families or clones. There is a range of methods to produce open-pollinated improved seed. The rate of improvement they provide increases in the sequence from seed production area (usually established in natural stands or mature plantations) through un-pedigreed seedling and clonal orchards, to tested, advanced-generation orchards.

Open-pollination seed production stands and plantations are well suited to exploit additive genetic variance (or general combining ability). The reduction in genetic variability in their resulting progeny is minimal, which is an added advantage early in a tree improvement program. Genetic gain can be increased by exploiting non-additive genetic variation (or specific combining ability) — for examples see Nikles et al. (1988). Not many tree breeding programs in the tropics have reached this stage, involving assessment of the value of crossing pairs of selected individuals.

Controlled crossing has limitations in terms of the amount of material produced. Its use is therefore often restricted to research: progeny testing, regenerating breeding populations, developing families of appropriate size for effective 'forward' selection (in population improvement) or for studies on hybridisation (Nikles 1992). If intended to produce operational planting material, controlled crossing coupled with 'bulk propagation' (i.e. vegetative multiplication at the young seedling stage of full-sib family material) can be used. Such a process has been termed 'family forestry' (Nikles 1992). Specialised seed orchards, such as hedged orchards, may be effective for controlled crossing on a large scale. Nikles (1992) describes three techniques which can be used:

i) Mass pollination after emasculation of the clone used as female parent. Here the Queensland Forest Service's work in producing seed of the *Pinus elliottii* × *Pinus caribaea* var. *hondurensis* F_1 hybrid is cited.

ii) Mass pollination without emasculation. Reference is made to the Queensland seed orchard of *Araucaria cunninghamii*. Here mass pollination is feasible because young orthotropic grafts abundantly produce female flowers annually for many years before they produce pollen (Haines and Nikles 1987).

iii) Supplemental pollination. Examples are from seed production of *Eucalyptus* hybrids in the Congo (*E. urophylla* × *E. grandis* and *E. urophylla* × *E. pellita*) (Vigneron 1991).

New possibilities for mass propagation of seed produced by controlled crossing will probably emerge in future, thanks to a better understanding of self-incompatibility and male sterility phenomena and the wider use of gametocides. There is a need to enhance research in this area. Genetic engineering is one possible technique for obtaining male-sterile trees. Male-sterile transgenic plants have already been obtained in several annual plants.

Vegetative propagation

Bulk propagation is used, in general, to multiply young seedling material of high genetic value, the production of which, by seed, is limited (i.e. selected provenances; selected full-sib families). Clonal forestry is particularly relevant in at least three types of situation: i) to propagate superior genotypes of unknown pedigree i.e. genotypes which are not reproducible by the sexual route, such as many natural hybrids; ii) to propagate material of known pedigree selected on a character with low heritability as for instance certain traits of wood quality; and iii) to propagate selected provenances and families sooner than a seed orchard could do, thereby increasing the genetic gain per unit time (Wong and Haines 1992).

Currently, rooted cuttings (and sometimes tissue culture, used as an aid to produce more responsive (rejuvenated) stock plants) are the foundations of most operational clonal plantings (Nikles 1992). Mature tissue material is, in general, much less responsive to true-to-type cloning than juvenile material. Therefore a constraint that has to be tackled with the clonal option is the need to rejuvenate the selected mature trees. Micro-propagation in vitro by tissue culture has potential for rejuvenating to some extent mature tissues especially throughout meristem culture, but there is a need for in-depth research to understand the physiological and molecular basis of rejuvenation. 'Aging effects' and the problem of regenerating entire plants from culture (de-differentiated cells and organised tissues) constitute major bottlenecks to progress toward wider development of vegetative propagation and the associated biotechnologies (genetic engineering) (Haines 1994).

The potential for rapid gain associated with clonal forestry has led to considerable interest in this technique during the last ten yr, and there are now extensive clonal plantation projects in several tropical countries, principally with eucalypts (mainly hybrids). There may be even more pressure to embark on clonal forestry in coming years due to progress in genetic engineering (e.g. Griffin 1996). Presently, transgenetic poplars are being evaluated in the field for insect and herbicide resistance (for example in France and the United States). There are plans to apply this technology to several tropical species of *Eucalyptus* used in pulpwood plantations.

Significance of Water Use and Nutrient Use Efficiency in Adaptation

As discussed in the previous section, the establishment and assessment of species, provenance or other genetic trials on sites of varying hydrological and nutritional status has permitted some selection of genetic resources for sites characterised by drought and/or low nutrient levels. In effect, genetic field trials test for 'adaptation' to the test site and (hopefully) other sites subject to similar conditions. The value of such field trials in selecting genetic resources for better management of soil, water and nutrients depends on a number of factors, some of which were mentioned in the previous section. Their effectiveness in selecting for adaptation to low water or nutrient availability also depends on the nature of the adaptation, which therefore requires further consideration.

Adaptation constitutes the response to changing environmental conditions so as to maximise fitness (Matyas 1989). Adaptation is therefore dynamic rather than a constant. Environmental conditions vary in both time and space, and at different temporal and spatial scales. The responses of organisms to variation at different scales is through a combination of phenotypic plasticity, genetic selection or migration (Stettler and Bradshaw 1994), with the relative importance of the three components of adaptation depending on the scale and magnitude of the variation. For example, an organism encountering spatial variation in water or nutrient availability will be subject to natural selection for adaptation to the prevailing conditions. If, however, there is marked variation in environmental conditions over a small spatial scale, natural selection for narrow adaptation is not effective, as the environment encountered by a germinating propagule has a high probability of being different from that experienced by the parents. Under such circumstances, fitness is maximised through selection for high plasticity. Thus tree species which naturally occur in highly variable environments are likely to exhibit higher phenotypic plasticity than species occurring in a narrower range of conditions (see

Chapters 3 and 4 for a discussion of spatial variability in water and nutrient availability in tropical soils).

Within a broad climatic zone, drought limits plant growth more than any other environmental factor (Kramer 1986). In particular, water deficiency is the most significant factor limiting early seedling survival and growth (Marshall and Maki 1946; Blake 1983). Considerable adaptive advantage is conferred to a genotype that can maintain turgor and physiological functions during drought stress (Morgan 1984; Turner 1986; Ludlow 1989). Plants may adopt two strategies to deal with water stress—dehydration avoidance or dehydration tolerance. The usual process for dehydration tolerance consists of stomatal closure, and a consequent reduction in photosynthesis (Brix 1962; Kramer and Kozlowski 1979), although there are various approaches to dehydration avoidance (Gullo and Salleo 1988). This strategy is common in many species of plants (Larcher 1980; Kozlowski et al. 1991). Dehydration tolerance, where plants maintain stomatal conductance and their rate of photosynthesis under increasing drought stress has been found to occur in some species (e.g. Gullo and Salleo 1988; Tan et al. 1992). Osmotic adjustment—the accumulation of solutes in response to water stress—may be one of the most effective dehydration tolerance mechanisms in plants (Blum 1989), although Fan et al. (1994) reported that elastic adjustment—reflecting the capacity of tissue to shrink—may be a more important mechanism for some species.

Osmotic adjustment can benefit droughted plants in different ways. A positive turgor is required for cell expansion and growth under drought (Cosgrove 1981) and is crucial for the continuance of most, if not all, biochemical, physiological and developmental processes (Jones et al. 1981). The lower osmotic potential would also promote water absorption in drying soil (Morgan 1984). An accumulation of water-compatible solutes, such as sugars and some amino-acids, may promote turgor maintenance and reduce cell damage in drought-stressed plants (Borowitska 1981), facilitating rapid recovery after water stress is relieved (Barlow et al. 1977; Tan et al. 1992).

There may be no particular energetic advantage of osmotic adjustment, compared with stomatal closure, in the short term (McCree and Richardson 1987). However, osmotic adjustment may be advantageous to plants in the longer term, since accumulated organic solutes can be re-metabolised after the water stress is alleviated. Thus, although dehydration avoidance is a form of adaptation to drought-prone sites which increases survival during periods of water stress, dehydration tolerance mechanisms may allow simultaneous selection for increased survival and faster growth. A positive correlation between dehydration tolerance and growth rates under periodic water stress has been noted for wheat (Morgan and Condon 1986), for the boreal conifer black spruce (*Picea mariana*) (Tan et al. 1992) and for *Eucalyptus camaldulensis* (Grundwald and Karschon 1982).

Variation in photosynthetic rates among provenances of the tropical legume, *Pterocarpus macrocarpus*, has also been found under artificial drought stress, indicating likely genetic variation in drought tolerance (unpublished ASEAN Tree Seed Centre/CIFOR data).

As was mentioned above, adaptation can occur both through genetic processes (natural selection or migration), and/or through phenotypic plasticity. For some species, for example black spruce and the subtropical *Eucalyptus grandis*, as well as some crop species, dehydration avoidance and/or dehydration tolerance has been found to increase if seedlings are subjected to repeated cycles of water stress (Fan et al. 1994; Kimani et al. 1994). This suggests that adaptation to drought-prone sites can be improved not only through genetic selection but also, to some extent, by cultural practice.

Physiological plasticity is also often observed in responses of trees to sites having low nutrient availability. For example, Boerner (1984) studied four temperate species growing on sites of different nutrient availability and pH. He found that all species demonstrated a plastic response to low nutrient availability, with greater leaf mass produced per unit N or P investment, proportionately greater resorption of N and P, and reduced leaching. These nutrient conservation strategies resulted in greater nitrogen growth efficiency in all species, and greater phosphorus growth efficiency in three of the species. Tree–nutrient relationships are usually strongly mediated by microbial associations, ectomycorrhizae being the major associate in the case of tropical trees. Lapeyrie and Hogberg (1993) suggest that an appropriate selection of fungal strain can overcome nutrient limitations to growth of tropical trees on many low fertility sites. However, much still remains unclear in the potentially complex three-way interaction of tree genotype × fungal genotype × site. For example, Grove et al. (1991) report neutral or even negative correlations between the efficiency of mycorrhizal strain in the nursery and the field for some *Eucalyptus* species.

Even less is known about the genetic responses of trees to sites affected by high heavy metal concentrations. Dickinson et al. (1991) review the evidence for tolerance of polluted sites by tree species. They conclude that although there is no evidence for genetic variation in tolerance, the possibility exists for some species. A more likely explanation for survival and growth on polluted sites, however, involves physiologically plastic responses, particularly avoidance strategies. Gill (1986) raised the possibility that long-lived perennials may benefit from somatic mutation in adapting to polluted sites, but evidence for this remains elusive.

Selection Methods for Water-use and Nutrient-use Efficiency

As for any characteristic with potential to be improved through a breeding program, a forester is faced with the choice of manipulating genetic resources or manipulating the environment. Improved success in afforestation of sites which are liable to water stress may be achieved through wise management of a cover crop. Especially early in the establishment phase, species forming a cover crop may compete with the tree seedlings for scarce water and/or nutrients. Fertilising such a plantation to alleviate nutrient stress may in turn exacerbate water stress if the competing vegetation responds to the increased nutritional status of the site.

In tree improvement through selection of genetic resources, a number of decisions have to be made concerning the use of these genetic resources. These decisions apply to the different levels of the genetic hierarchy, i.e.: species, provenance, family and genotype. The usual process of genetic selection for adaptation to plantation sites consists of the choice of species through field testing, or matching species' environmental requirements to known site conditions, followed by selection of provenances (i.e. populations or seed-sources) within species. More sophisticated plantation programs may progress further by selecting families within provenances, and even genotypes within families. Both family and genotype selection imply a planned field testing and seed orchard component in the plantation program.

The relative benefit of matching different hierarchical levels of genetic resources to site varies, depending on the amount of genetic variation within the hierarchy. Thus, differences in performance among species are very great due to the large genetic differences among species. The degree of variation among provenances tends to vary according to the ecological range of the species. Species restricted to narrow ecological and/or geographic ranges tend to exhibit relatively little provenance variation, whereas wide-ranging species are characterised by large provenance variation. For most tree species, most of the total genetic variation occurs among families and individuals within provenances. Thus, major genetic improvements can be made at the lower levels in the hierarchy. However, the rate of genetic improvement (or 'genetic gain') per unit cost or effort also depends on the ease of testing and selection. As mentioned above, exploiting variation at the family and individual levels usually implies a sophisticated program, requiring a higher degree of technical ability than selection of species and provenances.

In all genetic testing and selection programs, whatever their degree of sophistication, there is a need to balance two goals, which are usually conflicting—the need to make accurate predictions of the performance of the genetic resources being tested, and the need to do so quickly, in order to allow progress in the plantation program. For long-lived tree species, the conflict between the need for accurate selection and for rapid selection is particularly acute. Incorrect selection has long-term negative consequences, but accurate selection, especially for rotation-age characters, such as yield, is very time-consuming. There are several approaches to testing genetic resources, the efficacy of which depends on numerous factors including the species, traits being tested, range of test sites and accumulated information on the species. Various of these approaches will be discussed below.

Conventional field trials

Many thousands of field trials of tropical species and provenances have been established around the world. For example, a program of cooperative field testing of three species of tropical pine, initiated by the Commonwealth (now 'Oxford') Forestry Institute in the early 1970s, developed into a network of over 600 field trials in 65 countries (Pottinger 1994). Similarly, many species of Australian eucalypts and acacias have been established in an enormous number of trials throughout the tropical and subtropical world (see Boland 1989; Slee and Midgley 1991).

A standard field testing program, with emphasis on tropical conditions, has been described by Burley and Wood (1976). Conventional field trials offer a relatively straightforward approach, without the need for advanced technical skills, computing or laboratory facilities. If done correctly, they do however require substantial investments of time and money, and correct analyses and interpretation of these analyses is more complex than is often assumed. Field tests also yield accurate results very slowly, and the temptation to short-cut conventional field trials can have serious negative consequences. For example, the selection of a species to constitute a major component of a plantation program, based on growth data from a few years of age or less, may be very costly if late-rotation form or disease problems are subsequently discovered.

There are several possible approaches to reducing the time required for field tests while maintaining accuracy of selection. These include the use of existing data from arboreta and other trial plantings, which are especially useful in selecting species to be included in field trials (Burley and Wood 1976); cooperation with other countries or organisations having greater experience with the species of interest (Slee and Midgley 1991); and the use of data from pre-existing field trials. This last approach is conducive to the use of computer modelling, and is discussed in greater detail below.

Conventional field trials will continue to be a significant component of any genetic testing and selection program. As the amount of existing information increases and other approaches become more sophisticated, so the efficiency of field trials will also be improved.

Expert systems/computer modelling

This is potentially the most powerful approach to selection of genetic resources, and the most generalisable. A modelling approach can be subdivided into two possible types of model—those which model site conditions to known or inferred environmental distributions of species or provenances, and those which model observed responses, at any level in the genetic hierarchy, from existing field trials.

An example of the first approach is homoclime modelling, in which genetic resources are selected from environments most closely resembling those of the planting sites. Bioclimatic envelopes can be developed through computerised interpolations and used to predict performance in other areas (e.g. Booth and Jovanovic 1988). Continued improvements in methods to predict local climates from a dispersed network of climate stations, and incorporation of non-meteorological variables such as soil types, further improve the accuracy of predictions (Booth 1991).

The second modelling approach may consist of little more than large databases of performance in existing field trials, but a more advanced version of this approach is exemplified by PLANTGRO, which uses notional relationships between performance and numerous environmental variables to predict performance on an untested site (Hackett 1991; Booth 1996). The notional relationships may be derived from field trial data, knowledge of the natural distribution of a species, or even guesswork, depending on the level of available information.

Despite the enormous potential of modelling approaches, there are some limitations. In the case of models relating site conditions to known or inferred distributions, such models are incapable of predicting performance outside the range of distribution, i.e., extrapolation. We know however that many species and provenances perform very well outside the range of environmental conditions experienced in their natural range. The best example of this situation comes from the temperate species, *Picea omorika*. This species is endemic to a few remote valleys in the former Yugoslavia, where it is confined to highly calcareous, drought-prone soils. When planted as an exotic in the United Kingdom and elsewhere, however, it performs best on deep, acidic peats (MacDonald 1945). This could not be predicted from its natural distribution. There are many similar tropical examples. *Pinus patula* has a very limited natural distribution in central Mexico (Wormald 1975), but it performs very well on a wide range of sites around the world, many of which bear little resemblance to conditions in its natural range (e.g. Rahim 1986). Zobel (1972) noted that this species' adaptability could not be predicted from its natural distribution. Similarly, at the provenance level, many provenances of teak (*Tectona grandis*) do not perform as would be expected in field trials where teak is an exotic. For example, the provenance from Nilambur, India, where annual rainfall amounts to nearly 2600 mm, was the best-performing provenance in a trial at Gambari, Nigeria, where rainfall is only 1260 mm per yr, less than half the amount at Nilambur (Keiding et al. 1986). Where key environmental variables, such as rooting depth, vary at a relatively small spatial scale, the approach has limited value. Another problem is that this approach can be used only at the species and provenance levels. As noted previously, for almost all tree species, very high levels of genetic variation occur among individuals within populations (provenances), resulting in differences in performance that cannot be modelled.

The second modelling approach, using observed performance to make predictions for other sites, can be applied to all levels of the genetic hierarchy, and can be used for extrapolation. Its very significant drawback, though, is that it is dependent on the existence or establishment of extensive field trials, and this is not reasonable for most species. Approximations or even guesses may be used if existing data are not available, but this increases the likelihood of incorrect predictions with the potentially serious consequences noted earlier. There may also be a tendency to avoid this risk by limiting predictions to species for which adequate data exist, thus effectively greatly reducing the base from which selections may be made.

Early selection methods

Early selection methods can be considered under two headings—statistical methods, by which future growth predictions are based on performance early in the rotation, in some cases supported by data from 'retroactive' tests, and indirect selection methods. This latter category can be further divided into methods that rely on genetic marker loci, those that rely on physiological responses to environmental conditions, and those that use other observable traits, including morphological traits.

a) Statistical methods

As the growth of individual plants is subject to temporal auto-correlation, it is possible to make predictions about future growth rates based on past growth rates. As would be expected, the auto-correlation, 'age–age', or 'juvenile–mature' correlation tends to increase with increasing age and decreasing period between the observation age and prediction age. The use of retroactive tests, in which previously-tested genetic resources with known growth patterns are included in trials as a form of temporal control, can also improve the accuracy of predictions. The problem is therefore the same as that encountered by conventional field trials, in which the minimum age at which the age-age correlations are sufficiently strong to make reliable predictions is critical. This, in turn, is subject to estimation of heritability for the juvenile and mature traits. Methods have been developed to predict the minimum age at which predictions are likely to be sufficiently accurate (Magnussen 1988, 1991). Conditions which result in higher heritabilities of the observed and predicted traits will increase the correlation coefficient, and reduce the age of prediction (Magnussen 1988). Therefore, environmental control of such trials should be as great as possible, and for many field trials in tropical countries this may be difficult.

Magnussen (1991) demonstrated the value of Markov chain modelling in predicting highly complex dynamic processes, based on information on simple, basic processes at juvenile ages. He recommended that (for temperate species) two juvenile measurements 3 to 4 yr apart would be adequate to predict mature volume to an adequate degree of precision. He also noted that Markov chain modelling can easily accommodate genetic structure in the data. The advantages of basing predictions on data from closely-spaced trials, in which trees get locked into a hierarchy of domination and suppression that impedes change of rank, was also evident.

b) Indirect selection methods

Genetic marker loci

The term 'marker-aided selection' is widely and somewhat inconsistently used. Although often referring to the use of genetic locus markers, the term can in fact be used for any form of marker, or any of the indirect selection methods discussed here. Genetic marker locus selection is potentially a very powerful selection method at any level in the genetic hierarchy, but it is particularly useful at the family and individual level where most genetic variation resides, and where many other methods are not applicable. The method relies on the identification of a specific genetic locus, the expression of which can be observed either in the field or laboratory, and which is diagnostic of the presence of the desired trait. The marker locus may in fact be directly related to the trait under selection (in which case, it is not strictly 'indirect selection'), or may be completely unrelated but genetically linked to the trait.

The use of genetic marker loci is greatly facilitated by the existence of genetic linkage maps. For this reason, maps are currently being developed for a number of the most commercially-valuable tree species, including several species of North American conifer (e.g. Tauer et al. 1992), and Australian acacias (Byrne and Moran 1994). As genetic marker maps are better known for many agricultural crops, such genetic marker locus selection has already been successful in crop breeding. For example, marker loci have been identified for selection of transgenic calli containing a bacterial gene conferring resistance to economically significant diseases in tobacco (*Nicotiana tabacum*) (Guerineau et al. 1990; Carrer et al. 1991). Because of the inherent problems in breeding long-lived trees, marker locus-aided selection, particularly for quantitative trait loci, can solve many current problems in selection of tree genetic resources (Tauer et al. 1992), but as marker maps need to be developed for each species the development costs, with the present technology, are enormous.

Lande and Thompson (1990) investigated the optimum conditions for the use of marker locus-aided selection. They estimated that scoring genotypes on a few hundred marker loci may be required in the first generation of selection, but that this number could be greatly reduced in later generations. Strauss et al. (1992) have also highlighted some of the limitations to marker locus-aided selection. They point out that most of the successes in crop breeding to date have involved inter- and intra-specific hybrids, because of the linkage dis-equilibrium generated through hybridisation, and that hybrid breeding has little relevance to most tree crops. They also point out that the associations between marker and quantitative loci are limited to specific genetic backgrounds resulting from linkage equilibrium, and that the value of the associations is dependent on genotype × environment interaction at both loci. They suggest, therefore, that the optimum traits to benefit from marker locus-aided selection for tree species are likely to be high-value, low heritability traits, where selection intensities within families are high, compared with among-family intensities. These kind of traits, such as height and diameter growth, are subject to high genotype × environment interaction and tend to be controlled by many minor genes, rather than a few major ones, and may exhibit adverse genetic correlations with other important traits.

Finally, it should be pointed out that marker locus-aided selection does not eliminate the need for field trials. Field trials are required to establish the association between the marker locus and the economic trait, and may also be required to observe the effect of the marker locus—see further discussion of this below.

Physiological testing

The earlier discussion of the physiological basis of adaptation for water use and nutrient use efficiency indicates another approach to selection for these characters. If the physiological processes are well understood, rapid and simplified testing could offer ways to make effective early selections. As mentioned previously, genetic variation in dehydration tolerance or avoidance has been reported for a number of tree species, and for some of these there have also been associations demonstrated with productivity and/or survival.

In addition to the previously-quoted examples, genetic variation in water-use efficiency has been demonstrated in several species of acacia and eucalypt. For example, Kireger and Blake (1994) studied four species of African acacia, while Osorio and Perreira (1993) reported genetic variation at the clonal level in water-use efficiency of *Eucalyptus globulus*.

Studies on trees in natural environments can also be useful in understanding the potential role of physiological testing and its limitations. Franco et al. (1991) studied the tropical C3 tree, *Clusia minor*. They found interactions for water-use efficiency and photosynthetic rates with nitrogen and light levels. In low nitrogen conditions net daily CO_2 uptake and leaf area accumulation were only slightly affected by levels of photosynthetically active radiation, whereas at high N levels the differences were very large. Water-use efficiency also increased if seedlings were subjected to drought. They related these findings to the natural environment of the species, with high spatial variability of light and nitrogen levels, and periods of drought stress. Similarly, Field et al. (1983) studied the compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. They found that leaf nitrogen is a major determinant of photosynthetic capacity, and those species having the highest rate of photosynthesis per unit of leaf nitrogen also had the lowest rate per unit of water transpired. They proposed the ratio of photosynthesis to transpiration as an instantaneous measure of intrinsic water-use efficiency, and found that this correlated well with the natural conditions of the five species. Sarmiento et al. (1985) studied four woody species of the neo-tropical savannas that typically occur on nutrient-poor soils. They found that nutrient economy in these species was improved in two ways—firstly, by redistribution of nutrients from old to young tissues, and secondly, by minimisation of nutrient losses through a combination of low leaf wettability, low leaf cuticular conductance and renewal of leaves during the rainless season. They also, surprisingly, found a continuously high water flux, which they interpreted as being beneficial in maintaining leaf temperatures close to the optimum for photosynthesis.

The value of such studies on tree species in natural conditions is that they serve to highlight the complexity and diversity of physiological processes in trees. Although there are now many studies demonstrating the use of physiological testing in selection of genetic resources, especially for characters such as water-use and nutrient-use efficiency, there are also many studies where the relationships between physiological process rates and field performance have been poor. This may be partly due to the variety of strategies adopted by tree species to deal with stress conditions, and the interactions with other factors not necessarily controlled in experimental conditions. Thus, although physiological testing offers a valuable tool for rapid and accurate testing of genetic resources, a more thorough understanding of plant physiology is necessary for its most effective use. Also, in many tropical countries, the equipment and technical requirements for physiological testing may currently be a limiting factor.

Morphological markers

The use of morphological markers for indirect, early selection really combines characteristics of two of the methods previously described. The statistical approach to early selection uses observations on 'juvenile' traits as morphological markers of 'mature' traits. Usually morphological markers are characterised by presence or absence, and are usually believed to be under genetic control of a single or a few major genes. Similarly, morphological observations may merely constitute the most cost-effective approach to marker locus-aided selection.

One of the best examples of the use of morphological markers for early selection comes from horticulture. Chmir (1990) observed the bitterness of fruit resulting from hybridisation between sour cherry and bird cherry (*Prunus* spp.), and found that the presence of golden glands on the lower leaf surface in the hybrid seedlings, inherited from the bird cherry parent (*P. maackii*) was a clear indication of bitter fruit. Hybrid varieties with inedible fruit could therefore be selected at the seedling stage. Ganeshaiah and Uma Shaanker (1991) have also used morphological markers in genetic selections of some Indian tree species.

Synthesis

There has been a large investment in genetic testing and selection in the tropical world in the last three decades. This effort, together with rapid growth and short generation time, has led to outstanding improvements in the planting stock of several genera and species. There are of course many more candidate species, and this diversity presents greater opportunity and challenge than exists in temperate regions, especially because of the great diversity in the biophysical environment and soil.

Within the commonly-used genera such as *Pinus* and *Eucalyptus* there are instances in which particular species have been preferred to others because of their greater tolerance of environmental limitations. If those limitations are lessened, for example through fertilisation, the choice of genera and species expands; conversely if site resources are depleted, the range of genotypes which can be successfully grown contracts. There is thus an intimate relationship between site characteristics, cultural practice and the characteristics of actual or potential crop trees.

We have reviewed the methods available to match site characteristics with planting material, and to improve the latter. Conventional field trials will continue to be a useful and robust though time-consuming method of selecting genetic resources. Much-improved use can be made of results of field trials if they are complemented by details of the trial sites and collated in well-structured data bases. This information, and new analytical techniques, can help to choose species or provenances for testing, and can assist interpretation of test results. Increasing appreciation of the significance of water-use and nutrient-use efficiency in determining survival and productivity in forest plantations will ensure continuing effort to identify and develop improved planting stock for a range of sites. The use of marker locus-aided selection offers promise for the future. It is important that a considered breeding strategy be used to efficiently harness the genetic and material resources available to the socioeconomic objectives of the forest owners and/or the wider community; examples of strategies and plans for eucalypts are available.

In many countries, the government has been responsible for forest plantation programs because of the large amount of resources, of both land and money, required for broad-acre operations. However, just as agriculturists are now recognising that small farmers can be effective conservers of genetic resources as well as plant breeders, so too is there growing evidence from some countries that the small-scale private sector, whether in the form of farmers or entrepreneurs, can play an important role in afforestation. This private sector lacks the resources to support a genetic testing program, but is very effective at matching available genetic resources to specific sites. In some temperate countries, improved material has been made available to this sector by private sector and government-private sector cooperatives through which resources are pooled. Similar institutional arrangements may improve the matching of genetic resources to sites for tropical plantation programs, as well as assisting in providing optimum planting stock and subsequent management.

There is certainly a need to test new potential plantation species. This is particularly true at a time when increased international attention to the legal status of exotic germplasm, as well as to its environmental impact, is likely to make the use of exotics more subject to regulation and controversy. Indigenous forest species, which may be adapted to rather narrow ecological niches, have tended to be overlooked in the past in favour of broadly adapted, fast growing exotics. There is also a case for research on the physiological processes controlling water- and nutrient-use efficiency, and, at least for the most valuable plantation species, for research on developing genetic marker maps. More significant in the short term, though, is the requirement to make better use of knowledge from the many field trials already established, and to act promptly on this knowledge by making improved planting stock available to growers.

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3

The Biophysical Environment

J.J. Landsberg

Abstract

This chapter provides key background information on, and discussion about, the climatic conditions under which subtropical and tropical plantation forests are established. The atmospheric environment acts on plant communities through their leaves, so stand structure and architecture are discussed to provide the background necessary for understanding the micrometeorological processes involved in stand–atmosphere interactions. The most important of these processes are radiation absorption, which determines (potential) photosynthesis and hence plantation growth, and the energy balance. Characterisation of the energy balance allows calculation of transpiration from plantations; the transfer processes that govern the fluxes of heat and water vapour (and CO_2) are described. The hydrology of plantations is treated by consideration of the hydrologic balance equation.The Penman–Monteith equation, generally regarded as the best formula for the calculation of evaporation, is treated in some detail. In the final section a simple model that can be used to calculate plantation growth and productivity is presented. The model is soundly based in processes such as energy absorption by canopies, and includes terms for nutrition and water balance. It is proposed as a future alternative to classical site index and age-related growth curve methods of estimating plantation productivity.

CLEAR UNDERSTANDING of the way environmental factors act on, and interact with, plant communities is essential for predicting plant growth. This chapter outlines the biophysical processes that determine how the environment acts on plant communities, and indicates the measurements that will be most useful for evaluating the responses that might be obtained in field experiments designed to determine productivity or to test for differences between species, provenances or silvicultural treatments.

Plants grow by using radiant energy to convert CO_2 and water to carbohydrates. The efficiency of the process, i.e. the mass of carbohydrate produced per unit energy absorbed, is strongly affected by the nutrient status of the leaves, but if water is in short supply stomata close, CO_2 uptake is restricted or stopped and growth ceases. Furthermore, roots cannot absorb nutrients from dry soil. Therefore water is likely to be the factor that sets an absolute limit on whether trees can grow in an area or not, and the periods when growth can take place, while nutrition will be an important factor determining the efficiency of radiation conversion, and hence the rate of growth, when water is not limiting. Nutrition is dealt with in other chapters of this book, but we should note that environmental conditions influence the availability of nutrients because the rates of organic matter decomposition and nutrient mineralisation depend on the temperature of the litter layers during periods when they are wet; dry material decomposes very slowly.

An introductory section provides some general information about the characteristics of tropical climates in terms of rainfall, temperature, solar energy income and evaporation rates. In general the areas with which we are concerned have high temperatures throughout the year, with minimum temperatures never less than 10°C, and usually considerably higher. Rainfall varies. Radiant energy income is high although, because of cloud, not as high as in the arid and semi-arid subtropical regions. The climatic conditions covered by the graphs of Figure 3.1 span the range with which we are concerned. Clearly the actual location of areas in the tropics suited to plantation forestry depends on topography and soils as well as climate.

The atmospheric environment acts on plant communities through their leaves, so stand structure and architecture are discussed to provide the background necessary for understanding energy balance, radiation absorption and the processes by which CO_2, water vapour and heat are transferred between plants and the air. Micrometerological processes are considered in some detail, but with emphasis on providing simple, practically useful equations that can be used to analyse the interactions between plantations and their environment.

The rates of water use by plantations—or any plant community —are determined by the interactions between transpiration, driven by radiant energy and atmospheric humidity, and soil moisture, which in turn is dependent upon the balance between inputs from rainfall and losses by run-off, drainage and evaporation. As background to the treatment of stand hydrology I discuss the Penman–Monteith equation, derived from analysis of micrometeorological processes and now the most widely used equation for calculating and analysing transpiration. Plantation water balances are discussed in terms of the basic hydrological equation. The likely impacts of plantation establishment on hydrology at landscape level are considered in Chapter 5.

The penultimate section of the chapter presents a simple model of plantation growth and productivity, written in terms of dry matter production by stands in relation to energy absorption. It is unlikely that this model will, in the near future, replace the site indices widely used in forestry for many years, but the development of large areas of tropical plantations provides an opportunity to move away from that very circular method of evaluating site productivity towards a more rational, scientifically-based and—eventually—much more useful approach. The way this can be achieved is outlined.

The Atmospheric Environment

Climatic conditions (rainfall, evaporation, mean minimum and maximum temperatures and monthly average water balance, calculated as the difference between the average monthly totals of rainfall and evaporation) at four representative tropical locations are illustrated in Figures 3.1a to 3.1d. The data are long-term averages from the very valuable global data set provided by Müller (1982), although we must recognise that data of this type cannot always be expected to correspond closely to the actual conditions that will be encountered at particular locations. To achieve comparative results for stations round the world Müller calculated evaporation (E, mm month^{-1}) using Thornthwaite's (1948) equation, which is an empirical relationship based on temperature, although this is known to be inaccurate for particular locations, and particularly unreliable in regions of high humidity. We should also note that the simple subtraction of average evaporation from average precipitation is only a rough indicator of the water balance for the vegetation of a region. Soundly-based procedures for estimating evaporation (such as those used by Shuttleworth (1988)—see next paragraph) and plant water use are discussed in the sections on 'Heat and mass transport' and 'The hydrologic balance', and the physical and physiological basis for making locally useful water balance calculations is presented in 'The hydrologic balance' section.

Shuttleworth (1988) has presented the results of a micrometeorological study of evaporation in the Manaus region including, for reference, mean monthly precipitation data for 16 yr. The precipitation data are consistent with those given by Müller. Shuttleworth's evaporation measurements, made over a 25-month period, gave a mean value of 110 mm month^{-1} while the mean of the Thornthwaite estimates given by Müller is 137 mm month^{-1}. Assuming the Shuttleworth values are correct this indicates an error of about 25% in the values given by Müller, which suggests that the water balance line in Figure 3.1a should be about 25 mm higher. This would reduce both the period of negative water balance, and the severity of the deficit. However, there is also a difference in the radiant energy income measured by Shuttleworth and the values given by Müller. Back-calculating the average short-wave energy income (ϕ_s, using equation 4b, presented later) indicates that the ϕ_s values measured in Shuttleworth's study are about 20% lower than those tabulated by Müller. The differences are almost enough to explain the differences in evaporation.

A point that emerges from the comparisons made above is that long-term climatological data may not correspond closely to data collected at a particular point over a short time period. Detailed and reliable studies similar to that of Shuttleworth are not available for other locations so, to retain comparability with the other regions considered, Figure 3.1a has not been redrawn with Shuttleworth's evaporation figures and data describing the climates of the other areas discussed are used unchanged from Müller.

In terms of temperature and radiant energy income Manuas (Fig. 3.1a) is typical of the wet tropics. Temperatures fluctuate very little, either diurnally or seasonally, and incoming solar energy varies from about 15 to 20 MJ m^{-2} day^{-1}. The precipitation pattern is somewhat more variable than might be expected, with rainfall in the middle months of the year falling significantly below evaporation, giving rise to the negative water balance in the June–October period. If this is a realistic reflection of the water balance of tree stands there will be very little growth during this dry period.

Bujumbura, in Burundi (Fig. 3.1b), receives less than half the rainfall of Manaus (~ 850 mm per yr compared to almost 1900 mm). Maximum temperatures are very similar, but minimum temperatures are significantly lower, reflecting both the higher altitude and drier climate—one of the factors affecting minimum temperatures is the loss of radiant energy from the earth's surface to the atmosphere at night; the rate of loss is higher in dry than in humid areas. Although evaporation rates are slightly lower at Bujumbura than at Manaus the lower rainfall results in a long period each year with negative water balance. When the water balance is positive the excess of rainfall over evaporation is not large, so it is likely that soil water replenishment is limited. Any proposal to establish plantations in such an area should be preceded by a detailed analysis of the soil water balance, and hence the likely growing season; this analysis would have to take account of soil depths and water holding capacity as well as the temporal distribution of rainfall (see 'The hydrologic balance'). Trees used in such an area would be deciduous, or evergreen with high tolerance to drought.

The climate at Jamshedpur, in India (Fig. 3.1c), is a typical tropical monsoon climate. Winter minimum temperatures fall to about 10°C but average daily maximum temperatures reach almost 40°C in the early summer, when there is virtually no rainfall. The water balance at that time is, correspondingly, strongly negative. Heavy monsoon rains, beginning in May, last for about six months, when maximum temperatures fall slightly, to the values (around 30°C) typical of the wet tropics. During the monsoon period rainfall exceeds evaporation by large amounts. Total rainfall is less than at Manaus but, because of the high radiation during the dry early summer months total energy income is significantly higher. Trees planted in this area would almost certainly be deciduous, since leaf-shedding would be the mechanism most likely to allow survival through the dry period.

Singapore (Fig. 3.1d) is unequivocally wet; the climate is characterised by remarkable stability. Maximum and minimum temperatures, and incoming radiation, scarcely vary from month to month. Precipitation varies slightly but is always more than evaporation so the water balance is always positive. Trees for this area would be tropical evergreen, and soils selected for plantations would have to be well drained.

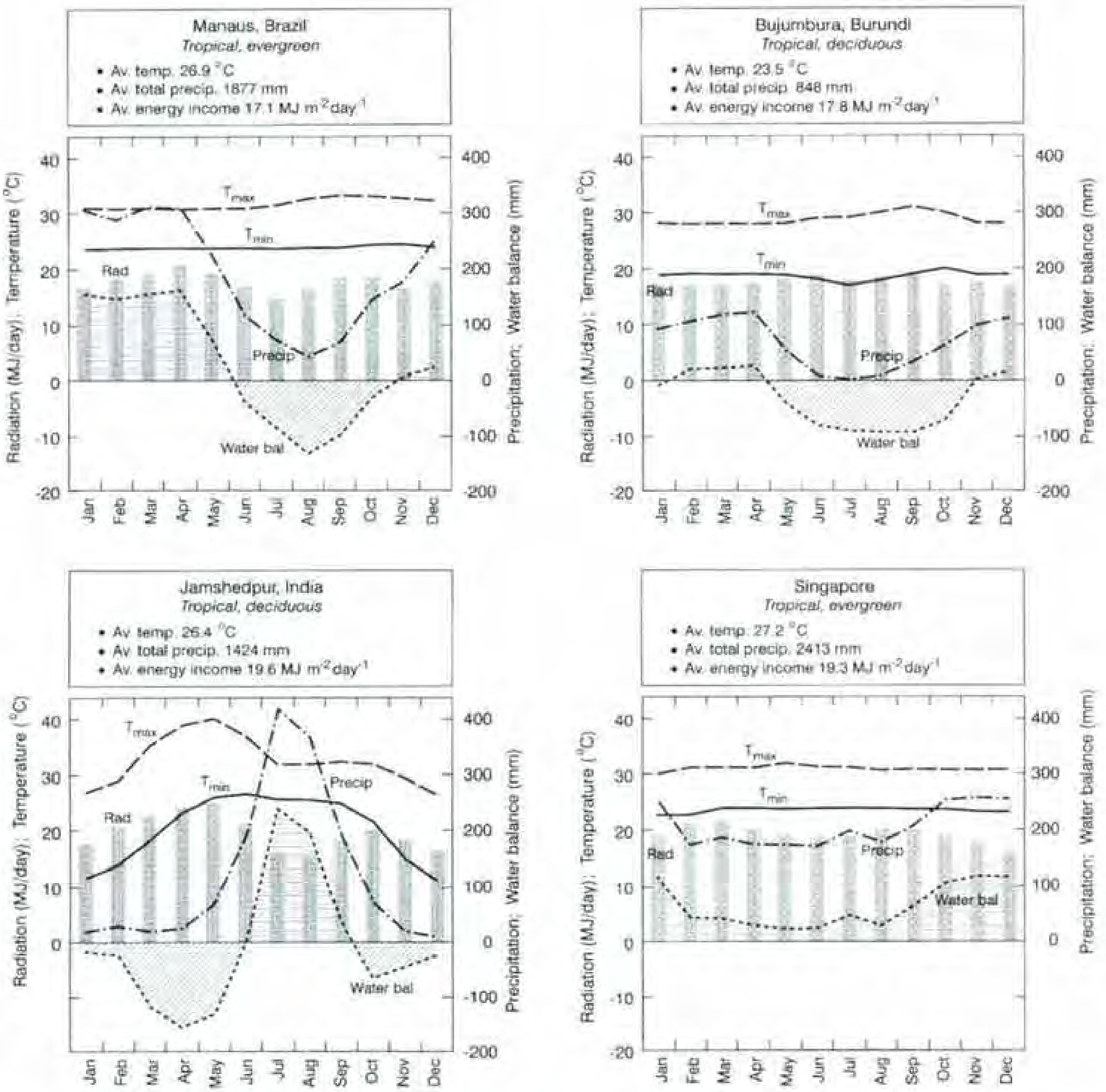


Figure 3.1 Annual course of climatic conditions at representative tropical locations: (a) Manaus, Brazil; (b) Bujumbura, Burundi; (c) Jamshedpur, India; and (d) Singapore. Radiation (columns) is short-wave solar. The water balance is calculated as the difference between precipitation (the dot-dash line) and total monthly evaporation (not shown). Data are from tables given in Müller (1982). The diagrams for Manaus and Jamshedpur are presented in Landsberg and Gower (1997).

The summaries of tropical climates provided in Figure 3.1 are intended to illustrate the variation that will be encountered, and the factors that will have to be considered, in relation to the establishment of plantations. It is essential that where such establishment is anticipated, or has begun, there should be appropriate, good quality weather measurements made in the area. These must include rainfall, on at least a daily basis so that temporal distribution patterns can be identified, temperature, humidity and wind speed measurements and, importantly, good quality measurements of incoming solar radiation. Radiant energy drives growth but there is widespread lack of appreciation of the need to measure it, and to use the data as the basis for analysing plant growth patterns. The sections on 'Micrometeorological Processes: Radiation absorption and energy balance' and 'Plantation Productivity' outline the analyses that can be done.

Canopy Architecture

The cover of leaves and branches that form the upper layer of a plant community is called the canopy; the vertical and horizontal distribution of foliage determines the canopy architecture. The transfer processes that determine the fluxes of carbon dioxide and water vapour to and from the foliage are strongly influenced by canopy architecture. These fluxes, integrated over time, provide a measure of the carbon and water balances of the plant community.

The canopy architecture of a stand is determined by the number, spacing, height and size of the trees. Clearly, in the case of plantations, when the trees are young the canopies consist of a series of individuals with crowns characterised by leaf arrangements typical of the species, and leaf mass (and hence area) influenced by nutrition and water status. In the early stages of growth the important component of the canopy is the crown size and leaf area of the individual trees. As the tree crowns begin to influence one another the rate and pattern of canopy development will be affected by the arrangement and stand density of the plantation: where the distance to neighbours is similar in all directions canopy closure will be reached sooner, with the same population of trees, than in situations where individuals are closer in the rows than between rows. In these cases the canopy will close along the rows before it closes across rows, so that for some period the plantation will behave, in terms of its energy interception characteristics and microclimate, like a hedgerow orchard. The duration of this period may have significant implications for weed control and erosion, which is exacerbated by raindrop impact on unprotected soil. Average crown size of individual trees will decrease as stand density increases. When trees are small enough not to interfere with each other their growth rates (in the absence of disease) are determined by the absorption of photosynthetically active radiation (PAR; see the section on 'Micrometeorological Processes') by the leaves— which depends on leaf area and arrangement—and their photosynthetic efficiency, i.e. the efficiency with which the leaves convert the absorbed radiation into carbohydrates.

From about the time of canopy closure the most important parameter describing the canopy is the Leaf Area Index (L^*)—the surface area of foliage per unit land area. L^* is a product of the average leaf area per tree and the number of trees. Foresters and researchers have, for a long time, used stem diameter (d_b) at 'breast height' (usually 1.4 m) as a measure of tree size, and it is generally possible to establish good empirical relationships between d_b—or, usually better, sapwood cross-sectional area—and foliage mass per tree (e.g. Whitehead 1978; Gholz et al.

1979; Kaufmann and Troendle 1981). Sapwood cross-sectional area reflects the amount of conducting tissue in the stems, and hence provides an indicator of the amount of foliage a stem is likely to be able to support. These useful relationships are likely to apply to tropical trees but should be established for various species, at different ages, growing under a range of conditions. Foliage area can be estimated from foliage mass (w_f) through the parameter specific leaf area (σ_f, $m^2\ kg^{-1}$). This varies between species, and indeed within a single species, depending on leaf age and growing conditions. Cromer et al. (1993) found that σ_f in *Eucalyptus grandis* in a fertilizer trial fell from values of about 30 $m^2\ kg^{-1}$ to 16–10 $m^2\ kg^{-1}$ over the first two yr of growth.

Although there have been few studies of the way the leaf area of individual trees, or of stands, varies with age, stocking and growing conditions, there is no reason to expect leaf area and canopy development patterns in tropical plantations to vary significantly from those observed in any other system. The study by Cromer et al. (1993) on *E. grandis* in the subtropics showed typical patterns. The trees were planted at 1100 ha^{-1}. Heavily fertilised plots reached canopy closure, with L^* about 5, within a year of establishment, while unfertilised plots had only reached $L^* \approx 1$ after 3 yr. Measurements by Kanazawa, Sato and Orsolino (1982) on the above-ground biomass and growth of *Leucaena leucocephela* in the Philippines indicated that plantations with stand densities that varied from 2650 to more than 12 000 stems ha^{-1} all had closed canopies by age 5 yr. L^* in these stands varied from about 1.2 to 5.5; Kanazawa et al. noted that these values are similar to those of deciduous broad-leaved forests in Japan and larger than values measured in *Albizzia falcataria* and *Gmelina arborea* in the Philippines. Foliage biomass varied from 0.68 to 3.63 t ha^{-1}; calculating foliage biomass per tree from their data revealed a clear tendency towards an inverse relationship—foliage mass per tree clearly declined as stand density increased.

Foliage development and longevity are both strongly influenced by water relations. When the rate of water loss by transpiration exceeds the rate at which water can be absorbed by the roots and transported to the leaves, water potential falls and the plants may become water stressed. The term is relative, since it is normal for water potential to fall during the middle of the day; this does not necessarily constitute 'stress', but if the condition develops so that the periods of low water potential are extended, then growth will be affected. Leaf growth is particularly sensitive to water stress. Bradford and Hsiao (1982), in their review of physiological responses of plants to moderate stress, noted that 'the first sign of (longer term) water stress is usually a restriction of foliage growth'. If this happens during the early stages of plantation growth there will be a strong feedback effect—the reduction in leaf area will result in less energy interception, hence less carbohydrate formation and less growth, including less leaf growth. Severe or prolonged stress not only results in reduction in leaf expansion rates, but also causes leaf senescence (see Pook 1985; Linder et al. 1987), which may lead to considerable modification to stand architecture. Borchert (1980) and Reich and Borchert (1982) demonstrated that leaf shedding, and the consequent improvement in the water balance of some tropical trees, triggered flowering, demonstrating that water stress can affect phenology. It is therefore important, in assessing the suitability of an area for plantation growth, to evaluate the probability of extended periods of drought and select species that will tolerate droughts of the severity that can be expected over periods corresponding to the expected life cycle of the trees.

Similar considerations apply to nutrition. The first and most obvious effect of fertilisation, particularly with nitrogen fertilizer in the presence of adequate water, tends to be an increase in foliage mass (Linder et al. 1987; Snowdon and Benson 1992). In plantations with closed canopies nutrient uptake may not increase much since only relatively small amounts of nutrient are immobilised in woody tissues; large foliage masses lead to competition for light and water, foliage losses may be high and the stand soon re-establishes a nutrient cycle in which the rate of release from decomposing litterfall almost matches the rate of uptake by the trees. However, in young plantations, before full canopy, the addition of nutrients will increase the rate of growth and affect the development of the canopy architecture.

Before canopies are closed, the soil between the trees is particularly vulnerable to erosion if it is bare, since there is no protection from raindrop impact and very little impedance to flow across the surface. Bare soil, when wet, also loses significant amounts of water by evaporation, although this may not be as much as would be lost by transpiration through cover crops or weeds between the rows. The relative risks and benefits of alternative management practices over this period require careful consideration.

Closed canopies vary in their depth, density and uniformity. Tree crowns may be flat or umbrella-shaped, so the depth of foliage from the top of the crown to the lowest foliage layers is relatively small; or they may have conical or ellipsoid shapes. Trees with flat or umbrella-shaped crowns may change their shape during their development cycle, with crown diameter increasing proportional to stem diameter. The concept of canopy depth—the distance from the (average) canopy top to the bottom of the green leaf layers—is particularly useful in describing simple canopies, such as those produced by plantations, because it provides a measure of the distance across which foliage is distributed. Clearly there is a considerable difference in the foliage density per unit canopy volume if the same L^* is distributed through very different lengths. It has been possible to establish empirical relationships between canopy depth, tree height and mean tree spacing for some temperate species (e.g. Liu and Burkhart 1993); this information would be useful if available for tropical plantations.

A closed canopy of reasonable extent (in terms of land area) essentially presents a continuous surface to the sky. The way this surface reflects radiation depends on its geometry and the reflectance properties of the leaves. The geometry of the upper layers of the canopy has considerable influence on air flow over the stand and the density, in terms of the volume of leaves and branches per unit volume of canopy, determines the way momentum will be absorbed from the wind and hence windspeeds inside the canopy. These considerations will be dealt with in some detail in the following sections.

Micrometeorological Processes

Radiation absorption and energy balance

Plant growth is driven by the amount of photosynthetically active radiation absorbed by the foliage and the (photosynthetic) efficiency with which the leaves use that radiation (photon flux, ϕ_p) to produce carbohydrates. PAR is the radiation in the visible wavebands (about 0.4 – 0.7 μm) of the solar radiation spectrum. In the tropics PAR as a fraction of ϕ_s appears to vary between about 0.5 and 0.62, the higher values occurring on cloudy days. The mean value is about 0.51 (Stigter and Musabilha 1982). If we were concerned with the calculation of photosynthesis *per se*, rigorous modern plant physiology would require that we deal in terms of the flux density of photons (μmol $m^{-2}s^{-1}$) rather than radiant energy, because photosynthesis is a photon-driven process, and its efficiency is measured in terms of moles CO_2 fixed per mole photons absorbed by the leaves. However, to avoid confusion, we will deal in energy units throughout this paper, even when considering radiation absorption in relation to dry matter production by canopies (see 'Plantation Productivity').

In principle, stand growth rates can be calculated using radiation interception models combined with models describing leaf photosynthesis rates. Such models have been written at various levels of complexity, dealing with canopy photosynthesis at time scales ranging from hours to seasons (see Wang, McMurtrie and Landsberg 1992). They are valuable analytical tools, but are generally too complex for use for stand management. We need only note some general principles here.

First, short wave (solar) radiation (ϕ_s) penetrates closed canopies either as direct beam or diffuse radiation. Beam radiation is directional, the angle of incidence on the canopy being a function of earth-sun geometry (latitude, longitude, time of day, time of year). The probability of a beam being intercepted by elements of a canopy, or of penetrating it, depends on the leaf area in the path of the beam and the average orientation of the leaves. Diffuse radiation comes from all parts of the sky and the probability of penetration through a layer of known leaf area is obtained by integrating the equation for beam penetration over all solar elevation classes. In the tropics the ratio of diffuse to total solar radiation ranges from about 0.1, under clear sky conditions, to 1.0 when the sky is overcast. The ratio will vary with location and season.

Second, leaves may be either sunlit or shaded, and the relative proportions will cause differences in rates of canopy photosynthesis: clearly sunlit leaves are more likely to be photon-saturated than shaded leaves. The equations for sunlit and shaded leaf area are given by Norman (1982) and also presented in 'user-friendly' form by Landsberg (1986).

The most useful general equation for calculating radiation interception by canopies is Beer's Law, which describes the attenuation of radiation through a homogeneous medium. It can be derived from analysis of the path of beams through foliage (see Norman 1975) and, strictly, only applies to canopies if assumptions about the random distribution of leaves and spherical leaf angle distribution are met. However, when we are concerned to estimate the radiation absorbed over periods of days, weeks or seasons, then the integration over time and the averaging of direct and diffuse beam radiation, as well as leaf movements, allow the equation to be applied with little error. Beer's Law is written in the form

$$\phi_s(z) = \phi_s(0) \exp(-k.\, L^*(z)) \qquad (1)$$

where z denotes depth in the canopy, $\phi_s(0)$ is the net downward flux through the plane of the canopy top (i.e. after accounting for reflection), k is an extinction coefficient and $L^*(z)$ is the leaf area index between canopy top and level z (Fig. 3.2a). To use Equation (1) we require a measurement, or good estimate, of short-wave incoming solar radiation (ϕ_s) and a value for the extinction coefficient, k. Although k can vary between about 0.3 and 1.5 a value of 0.5 is a good approximation for most tree species (Jarvis and Leverenz 1983). It is worth noting the implication from Equation (1) that, since exp (-3) ≈ 0.05, with k = 0.5 a canopy with leaf area index (L^*) of about 6 will absorb 95% of incident radiation, and if ϕ_s = 18 MJ day^{-1} a canopy with L^*=5, for example, will absorb (18 – 18 (exp –0.5 × 5) = 18 – 1.48 ≈ 16.5 MJ day^{-1}.

When we are concerned with canopies that are not closed, the calculation of radiation absorption becomes more complex, particularly if the objective is to estimate absorption over short periods. For those concerned to do this, a paper by Charles-Edwards and Thornley (1973) describes a model of radiation absorption by a single plant. Charles-Edwards and Thorpe (1976) provide the equations needed to calculate radiation interception by a hedgerow system. They dealt with an apple orchard, but the analysis is directly applicable to any trees planted in rows which have not formed a closed canopy. Landsberg (1986; p.49) provides a useful approximate method for calculating radiation absorption by incomplete canopies: the amount of short-wave radiation reaching the ground (ϕ_{sg}) is given by

$$\phi_{sg} = \phi_s(0)\,(\zeta_g + \zeta_f) = \phi_s(0)\,(\zeta_g + \exp(-k.\, L^*_l)) \qquad (2)$$

where ζ_g and ζ_f denote the proportion of ϕ_s transmitted through gaps (or between rows) and through the trees themselves, i.e. not intercepted by foliage. The gap fraction for the plantation as a whole is a/A, where a is the (downward) projected area of the trees, and A is total area (see Fig. 3.2b), so it can be estimated from measurements of canopy spread. L^*_i denotes the leaf area index of the individual trees relative to a and k, as before, can take a value of 0.5. The energy absorbed by the trees is $\phi_s(0) - \phi_{sg}$. So, as a first approximation, the energy absorbed by an incomplete canopy can be estimated as

$$\phi_s(0) - (\phi_s(0)\,(a/A) + (1 - a/A)(\,\exp(-k.\,L^*_i))).$$

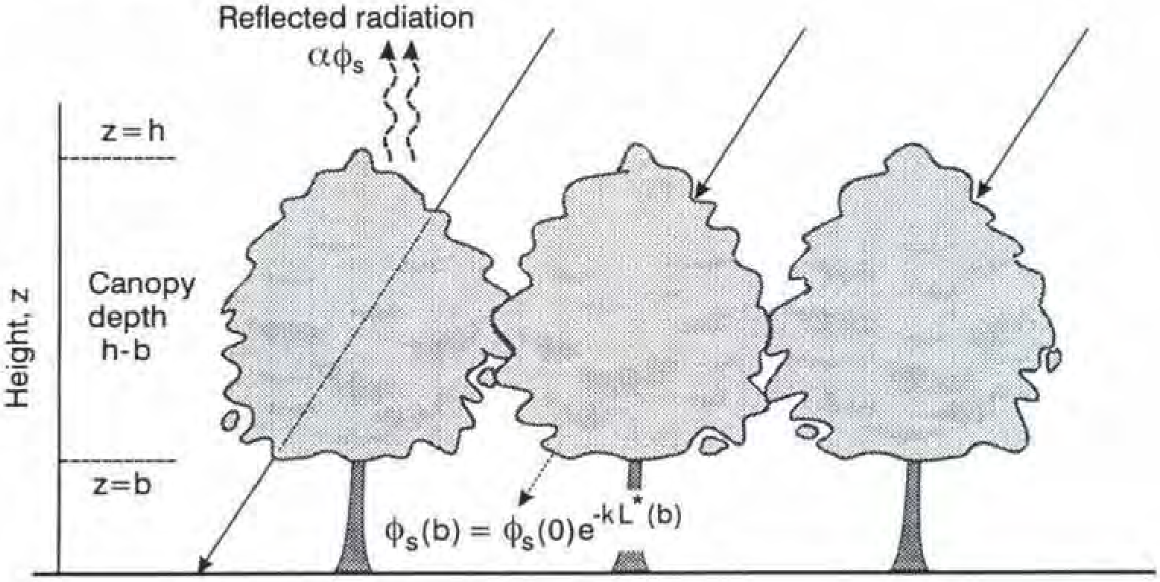
It would be valuable, in studies on the growth of tropical plantations, if measurements could be made of the energy absorbed by the stands during their development and after they have reached the closed canopy stage. Such measurements will allow the testing and parameterisation of the simple models presented here. They require a reference measurement of ϕ_s and measurements of $\phi_s(z)$, where z may be near the ground within the plantations (see Fig. 3.2b). Measurements of $\phi_s(z)$ can be made with linear radiometers or arrays of small sensors (see Torquebiau 1988).

Only a small fraction of the radiant energy absorbed by plant canopies is used in photosynthesis; most of it goes to warming up the ground, the trees or the air, or to evaporating water from the ground or plants. The radiation balance of a stand—or any surface—is given by

$$\phi_n = (1-\alpha)\,\phi_s + \phi_L \qquad (3)$$

where ϕ_n is the net radiation—the energy retained by the stand, α is the albedo or reflectivity of the surface—the fraction of incident short-wave radiation which is reflected from the surface, and ϕ_L is the long-wave balance—the difference between the upward flux of long-wave radiation which any surface with a temperature above absolute zero emits, and the downward flux from the sky, which is not at 0°K.

Values for α have been measured for many natural surfaces. For plant canopies they range from about 0.25 for smooth pastures to about 0.1 for coniferous forests. Pinker, Thompson and Ek (1980a) obtained average daily values of $\alpha \approx 0.13$ for a tropical evergreen forest in Thailand, with strong dependence on solar angle, so that there was significant diurnal variation on clear days (see also Pinker 1982). Shuttleworth et al. (1984b), who made measurements over Amazon forest, also observed a dependence of albedo on solar angle. They obtained a mean value of $\alpha \approx 0.12$ at a solar angle of 43.8°. These results can almost certainly be applied to closed canopy tropical plantations. Pinker et al. (1980a) also made measurements over a grassy clearing in the forest, where the albedo was about 10% higher than over the forest canopy. This provides a guide to the values that can be expected from plantations that do not have closed canopies. A valuable analysis of


a Closed canopy

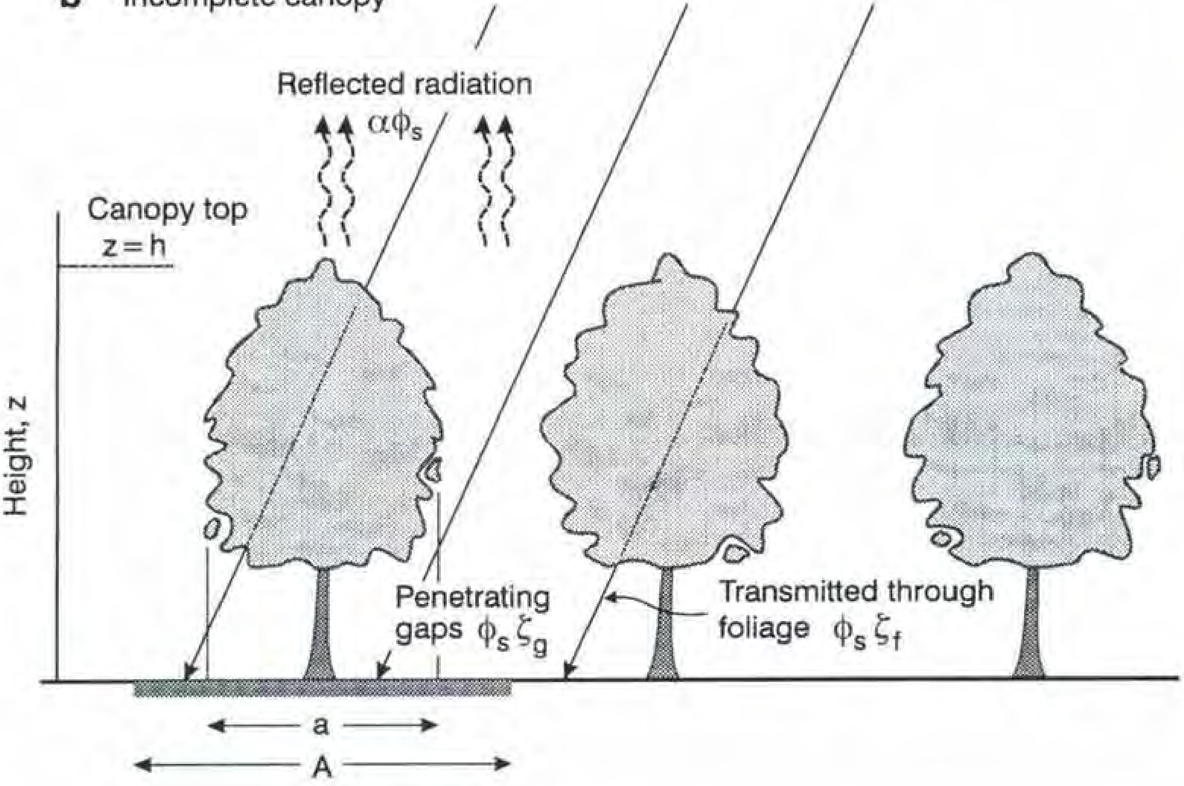

b Incomplete canopy

Figure 3.2 Diagrammatic illustration of radiation absorption by a closed canopy (Equation 1; Fig. 3.2a) and an incomplete canopy (Equation 2; Fig. 3.2b) net radiation flux per unit length of orchard row, where the canopy was closed along the rows but not across them, was provided by Thorpe (1978).

Values for $(1 - \alpha)$ and for ϕ_L in eqn (3) are commonly obtained by regression of ϕ_s on ϕ_n. Pinker, Thompson and Ek (1980b) established such regression relationships separately for each of 5 months. The values of $(1 - \alpha)$ and ϕ_L did not vary greatly from month to month. Using the overall averages the relationship was

$$\phi_n = 0.88\,\phi_s - 54 \qquad (4a)$$

where the units were W m^{-2}. Shuttleworth et al. (1984b) obtained

$$\phi_n = 0.86\,\phi_s - 35 \qquad (4b)$$

The values in these relationships indicate $\alpha = 0.12$–0.14—consistent with the albedo measurements. These relationships, although derived from hourly flux values, can be applied to daily totals, remembering that W m^{-2} = J m^{-2}s^{-1} so that, to calculate ϕ_n for a day the intercept value (54 or 35—say 45) must be multiplied by the number of seconds between sunrise and sunset. For example, assuming a 12-hour day, with $\phi_s = 18$ MJ (see data in 'The Atmospheric Environment'), then

$$\phi_n = 0.88 \times 18 \times 10^6 - 45 \times 12 \times 3600$$
$$= 13.9 \text{ MJ},$$

which is the amount of energy available for increasing the temperature of plants, soil or air, or for evaporation. Measurements of net radiation should be made above plantations wherever possible.

The conservation equation describing the partition of ϕ_n into latent heat (evaporation or transpiration — λE, where λ is the latent heat of vaporisation of water), sensible heat (H) and heat stored within the stand (G), is

$$\phi_n = \lambda E + H + G \qquad (5)$$

so that, given values for ϕ_n, solving Equation (5) for λE would provide estimates of the rates of water use by plant stands. The basis for these calculations is presented in the next section, and a 'working' equation for calculating transpiration is presented in the section on 'The hydrologic balance'.

Heat and mass transport

Transport processes

To solve Equation (5) we need some simple expressions for the sensible and latent heat fluxes, H and λE, in terms of quantities that are easily measured. Such expressions must be based on a physical description of the way heat and moisture (or any other 'scalar', like CO_2) diffuse in the atmosphere.

When air is very still, diffusion takes place by molecular movement and the rate of diffusion is given by the product of molecular diffusivities (a property of the air) and the gradient of scalar concentration. For example, we may write

$$H = -\rho\, c_p\, (dT/dz)\, K_h \qquad (6)$$

for the vertical flux of heat, where dT/dz is the gradient of temperature T with height z, ρ is air density and c_p is the specific heat of air; and

$$\lambda E = (\rho\, c_p / \gamma)\,(de/dz)\, K_v \qquad (7)$$

for the vertical flux of water vapour. The new symbols in (7) are the psychrometric constant γ and vapour pressure e. (Values of ρ, c_p and γ, with other useful physical constants and variables, can be found in Monteith and Unsworth 1990).

Unfortunately, most of the time air is not still but in turbulent motion, so the instantaneous wind speed is varying rapidly in time and space. This movement is much more efficient than molecular motion as a means of diffusing scalars. Nevertheless, in the air above a canopy we can still use Equation (6), but must replace $K_{h,v}$, the molecular diffusion coefficients, by $K_{T,q}$ the turbulent diffusivities. Typically $K_{T,q} \approx 1000\ K_{h,v}$ and is not a property of the fluid but of the flow, so it takes different values under different flow conditions and at different heights.

To understand the reason for this we need to understand what is driving turbulence. When wind blows over the ground, the molecules of air in contact with any solid surface (soil, leaves, branches) are stationary (aerodynamicists call this the 'no-slip' condition). Some distance above the surface the windspeed will have some relatively large value, so in between the surface and that level there must be a region of wind shear where, in any layer, air at a higher level is moving faster than the adjacent layer just below. At all but the lowest speeds this situation is unstable and generates turbulence—eddies and gusts of air at all scales—that efficiently mixes the atmosphere.

As the wind blows over the surface it 'drags', or exerts a force on the ground and plants i.e. there is a flux of momentum to the surface (by Newton's laws flux of momentum = force). The strength of this momentum flux is related to the intensity of the turbulence produced by the wind shear. As in the case of heat and moisture it is the turbulent eddies that transfer the momentum of the faster-moving air layers at higher levels to the slower moving layers below, and eventually to the surface (forest, plantation...).

Above the forest this flux is expressed in the same way as the scalars in Equations (6) and (7):

$$\tau = \rho\, K_M (du/dz) \qquad (8)$$

where τ is the kinematic momentum flux, more often called the shearing stress, and u is wind speed. Equation (8) allows the use of some well-known results to write a simple expression for K_M. Then, making the assumption that $K_M = K_T = K_Q$, it provides a method of solving Equation (5) (see below).

It is convenient, at this stage, to introduce another quantity, the friction velocity u_*, defined as

$$\tau = \rho\, u_*^2 \qquad (9)$$

The expression for K_M, K_T and K_q is then

$$K_T = K_q = K_M = k\, u_*\, z \qquad (9)$$

which states that the turbulent diffusivities for heat, water vapour and momentum above the canopy increase with height and with the square root of the drag of the wind on the surface. k is a constant of proportionality, known as von Karman's constant. It has a value of 0.4.

Two more points must be made before we use these formulae as the basis for a practical solution to Equation (5). The first is that wind shear is not the only means of producing turbulence and the mixing it engenders. Bouyant forces can do so just as well. If the ground or canopy is hot (heated by the sun) the air in contact with the surface is warmed, expands and rises to be replaced by cooler air from above, generating turbulent mixing in the process. If the canopy or ground is cooler than the air (e.g. if it has been cooled by radiation at night) then the denser air is at lower levels and extra turbulence must be generated by wind shear to stir it up. Hence, buoyancy can enhance or decrease turbulent mixing, depending on whether the conditions are unstable (day) or stable (night). There are well-understood equations for adjusting the diffusivities to take account of buoyancy effects, however, the adjustment factors are different for K_T, K_q and K_M, so that the equalities no longer hold if buoyancy is important. The variable u_* appearing in Equation (8) provides an indication as to when buoyancy becomes a matter for concern. Over rough surfaces like forests u_* is proportional to $u(z)$, so that, when winds are moderate or strong, most turbulence is generated by shear and buoyancy effects are less important. In still air or light winds buoyancy-generated turbulence can be the main source of mixing and must be taken into account.

The second major point to make is that expressions like Equations (6) and (7) do not work within the canopy because a series of other processes, including the precise form that turbulent eddies take and the proximity of the trees, change the way eddies are produced so that turbulent diffusion is no longer analogous to molecular diffusion. Even just above the canopy the effects that cause problems within the canopy also cause the equality $K_T = K_q = K_M$ to fail, even when buoyancy is unimportant.

(The theoretical development outlined in this section is given in detail by Kaimal and Finnigan (1994), where a treatment of the corrections for stability is also given).

For all conditions where $K_T \approx K_H$, we can take the ratio of Equations (6) and (7) and cancel the eddy diffusivities to obtain the so-called Bowen ratio:

$$\beta = \gamma\, dT/de = H/\lambda E \qquad (10)$$

Returning to Equation (5) in the previous section, if we ignore G (generally justified over periods longer than a day) we can now use β to obtain

$$\lambda E = \phi_n/(1+\beta) \qquad (11)$$

so that, given values for β and ϕ_n we can solve for λE. In principle, values for β are relatively easily obtained experimentally by using Equation (10) in finite difference form ($\beta = \gamma \Delta T/\Delta e$), and measuring temperature and vapour pressure gradients across some height difference (Δ), which may be quite large, so that differences in scalar concentrations across it are also reasonably large and easy to measure. Restrictions to this method are imposed by the requirement that both sets of measurements should be made high enough above the canopy for the assumptions about turbulent exchange to hold; by the requirement that buoyancy is not causing significant differences in the eddy diffusivities, and by the requirement that both sets of measurements should be made within the layer of air above the stand that reflects the properties of the stand, i.e. within the boundary layer of the stand. Air flowing across the stand from elsewhere will carry the properties of the surfaces across which it has passed, so measurements made in that airstream will not provide information about the processes taking place in the stand of interest. These requirements will restrict the use of the Bowen ratio in plantation research, but β is a valuable and informative parameter which has been widely used and measured in research on forest micrometeorolgy and water use. It can also be derived from the Penman–Monteith equation presented later (see Thom 1975; Kaimal and Finnigan 1994).

Pinker at al. (1980b), who made their measurements in a monsoonal rainforest (annual rainfall 1500 mm), found Bowen ratios of 6.38 in January, a dry month, and 0.45 in June, during the rainy period. Shuttleworth et al. (1984a) found that the energy used for evaporation by the Amazon forest was about 0.7 ϕ_n which, from Equation (5), with $G = 0$, and (10), corresponds to a Bowen ratio of 0.43. This can probably be taken as the lower limit for β, hence the upper limit for energy use by evaporation. There is, theoretically, no upper limit for β, since if stomata are closed (see below) in a dry canopy, so that λE approaches zero, β will approach infinity. Very high values of β may occur in deciduous stands in the dry part of the year in monsoon areas, but for stands with green foliage the value of $\beta = 6.4$ measured by Pinker et al. is probably among the highest likely to occur. Inserting this value in Equation (11) gives $\lambda E = \phi_n/7.4$, i.e the energy used in evaporation is about $0.14R_n$.

The discussion so far has been concerned with transport of heat, water vapour and CO_2 in the air layers above canopies where, at least in the daytime, flow is generally turbulent and one-dimensional equations can be used to calculate exchange processes.

Heat and mass transport processes within canopies are more complex. All the leaves in canopies exchange heat and water vapour with the air surrounding them, and each leaf must satisfy the leaf energy balance. The exchange processes between leaves and air depend on wind speed, leaf shape and arrangement (mutual shelter), since these factors determine the leaf boundary layer conductance, through which gaseous exchange takes place.

The equation governing the flux (F_l) of CO_2 and water vapour from inside a leaf to the external air can be written (using resistances, which are more convenient than conductances in this expression)

$$F_l = (c_i - c_a)/(r_b + r_s) \qquad (12)$$

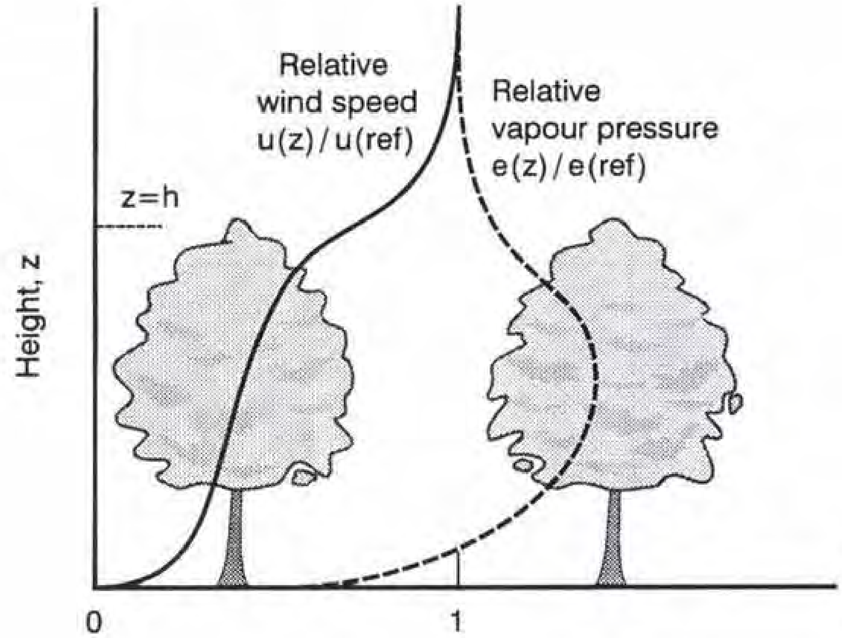
where c_i and c_a are the internal and external (ambient) concentrations of water vapour or CO_2 and r_b and r_s are boundary layer (aerodynamic) and stomatal resistances, respectively. The corresponding conductances (g_a and g_s) are $1/r_b$ and $1/r_s$ and the 'overall' conductance for water vapour $g_v = 1/(r_b + r_s)$. Writing Equation (12) for heat transfer, c_i and c_a become leaf surface and air temperatures respectively, and r_b becomes r_h (hence g_h). (Stomatal conductance (g_s) plays no direct role in heat transfer.)

Boundary layer conductance is inversely (non-linearly) related to windspeed, but it is usually much higher than stomatal conductance, which therefore tends to be the most important determinant of leaf–air exchange rates. However, because of the low wind speeds in the tropics, particularly within canopies (see below), and the large leaves sometimes found there, this is not always the case (see Grace, Fasehun and Dixon 1980). Detailed general treatments of the leaf energy balances are provided by Landsberg (1986) and Jones (1992).

The momentum, or shear stress, exerted by wind on canopies is absorbed by the canopy elements (leaves, branches etc.) so that the rate of attenuation of wind speed in a canopy is determined by the density of its elements. In very sparse or young stands, air flow will be affected more by the underlying vegetation or ground surface than the trees, but as tree density increases, or the trees get larger, mean wind speeds in the canopy are reduced and the wind profile is displaced upwards so that, in dense canopies, the effective surface for the wind profile above the canopy is the mean level of momentum absorption within it. The resulting in-canopy wind profiles have characteristic shapes (see Fig. 3.3) illustrated for tropical forests by the data of Thompson and Pinker (1975), who measured wind speeds within a forest and in a clearing. Estimates of air flow rates in canopies are most likely to be required in association with studies on photosynthesis and leaf evaporation rates, for example as a basis for work on water relations. Such estimates may be important in young canopies, before closure.

The humidity of the air inside plant canopies tends to be higher than above them, because of the transpiration from leaves and the relatively inefficient transfer processes from the bulk air in the canopy to the air above. Typical temperature and humidity profiles are shown in Figure 3.3.

a Incomplete canopy



b Closed canopy

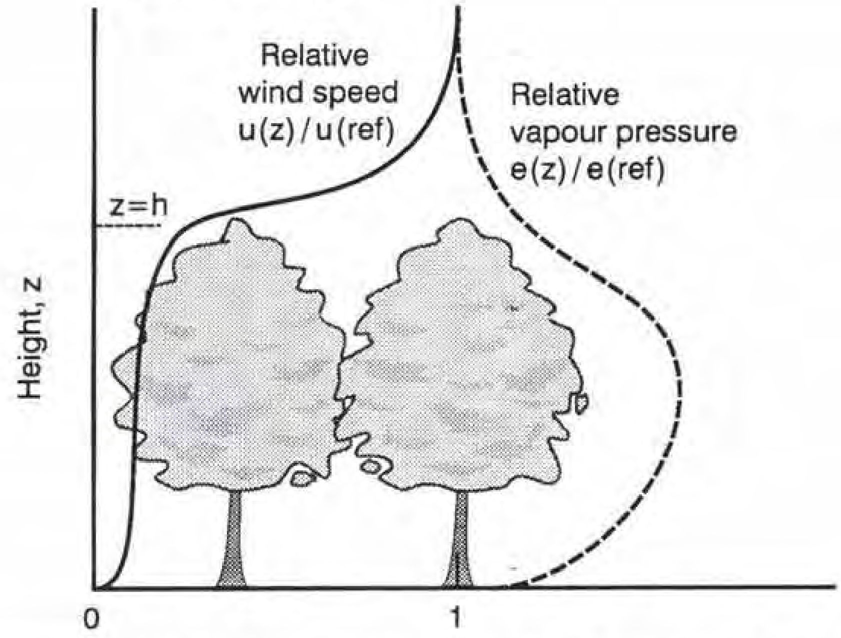


Figure 3.3 Typical windspeed and vapour pressure profiles for an incomplete and a closed canopy. Note that windspeed attenuation in the closed canopy is much more rapid than in the incomplete canopy, because the greater density of canopy elements results in much more rapid absorption of momentum. Vapour pressure in the incomplete canopy is sketched as reaching lower values near the ground than in the closed canopy for two reasons: i) the ground surface under that canopy is likely to be drier than under the complete canopy, and ii) even if the surface is wet, the higher windspeeds and hence more efficient transfer processes under the incomplete canopy would create a steeper vapour pressure gradient near the ground. In both cases the high vapour pressures in the main foliage zone would be caused by transpiration there.

Stomatal regulation

Stomata are at the interface between leaves and the air, and provide the means by which plants can control their intake of CO_2 and their rates of water loss. Consequently there is a vast body of literature on stomata and the way they function, and there have been a great many attempts to model stomatal behaviour. The most recent models for the stomata of C_3 plants include treatment of the interactions between boundary layers and the responses of stomata to photon flux, CO_2 concentrations and air humidity. In general, stomata open in response to increasing photon flux, tend to close at high CO_2 concentrations and open (g_s high) at high air humidity, closing as the vapour pressure deficit of the air (D) increases. A detailed interactive model, and discussion of its implications, is presented by Collatz et al. (1991); Leuning (1995) has recently provided a critical appraisal of the 'state of the art' in this area. However, these thorough physiological treatments are of somewhat limited value for many applications, and simpler models are often required. In this respect the more empirical model described by Jarvis (1976), and a model of similar form, with fewer parameters, described by Thorpe, Warrit and Landsberg (1980), are useful.

There is far less information on the stomatal conductances and responses of tropical than of temperate trees, but dry-season studies on *Gmelina* and teak by Whitehead, Okali and Fasehun (1981) showed that the values are much the same as those found in temperate trees, and the stomatal responses are similar. Whitehead et al. fitted the Jarvis model to their data. In a follow-up study, in the wet season, Grace, Okali and Fasehun (1982) noted some differences in stomatal responses, and commented on the fact that the conductance values they measured were high relative to those usually observed in temperate vegetation. We would expect daytime values of g_s to be high in the wet tropics—or in wet seasons in the monsoonal tropics—because of the generally high air humidity, particularly within canopies.

Where information on tree water-use rates is required (an area that is likely to be of considerable interest, particularly in climates with significant periods of negative water balance), measurements of g_s will be useful, although I would not recommend commitment of large research resources to these: as noted above stomatal responses are among the most intensively researched phenomena in plant physiology; field measurements are difficult to make well, despite the commercial availability of good quality porometers, and the results seldom provide much in the way of new insights. It is arguably more important to make good environmental measurements and to get good estimates of the leaf area of stands. Plantations, particularly before canopy closure, have much in common with orchards; the papers by Landsberg, Powell and Butler (1973), Landsberg et al. (1975) and Butler (1976) provide useful treatments of orchard micrometeorological measurements and analysis of the factors governing responses to environmental factors at the leaf-canopy level, including estimates of transpiration rates based on analysis of the leaf energy balance by Butler. They contain much that will be valuable if applied to tropical plantations.

For research into plantation performance, and environmental factors causing variation in tree growth patterns, the most generally useful measurements would be of radiation (as noted earlier), wind speeds above and within the canopy—to provide descriptive data—air temperatures, humidity and rainfall. There will seldom be much value, in relation to plantation establishment and management, in detailed studies of wind profiles above and within canopies in plantations—these are the realm of specialist research designed to increase our understanding of the mechanisms underlying the transfer processes.

The hydrologic balance

The hydrologic balance of any plant community is described by the same, completely general, equations. The only way in which tropical plantations will vary is in the relative importance of the different components of the water balance equation.

The basic hydrological equation is

$$\Delta\theta_s = R_f - (E_{int} + E_t + q_R + q_D) \qquad (13)$$

where $\Delta\theta_s$ is the change in soil water content in the root zone (see Fig. 3.4), R_f is rainfall, E_{int} and E_t denote the evaporation of water intercepted by foliage, and transpiration, respectively, and q_R and q_D denote surface runoff and drainage out of the root zone.

Equation (13) is a simple mass conservation equation and applies over any specified time interval. The amount of water that can be stored in the root zone depends on the soil water holding characteristics and the depth of soil exploited by the roots. Soil water storage capacities are characteristically in the range 100 – 200 mm m^{-1}. If the soil is saturated (the upper limit of soil water holding capacity has historically been called 'field capacity'—a useful, but not well-defined concept) additional rainfall will run off or drain through; it will not be available for utilisation by the trees. There are also strong interactions between rainfall intensity and infiltration rates: some soils may not be able to accept high intensity rainfall, considerable amounts of which may be lost as runoff even when the soil is not saturated. It is essential that the soils on which plantations are to be established should be characterised in terms of their physical properties, and particularly their infiltration and water-holding characteristics.

The rate of extraction of water from the root zone depends on the rate of transpiration (see below), and the capacity of the trees to sustain that rate, which will decline as soil water content diminishes. Root depth and exploitation of the soil,

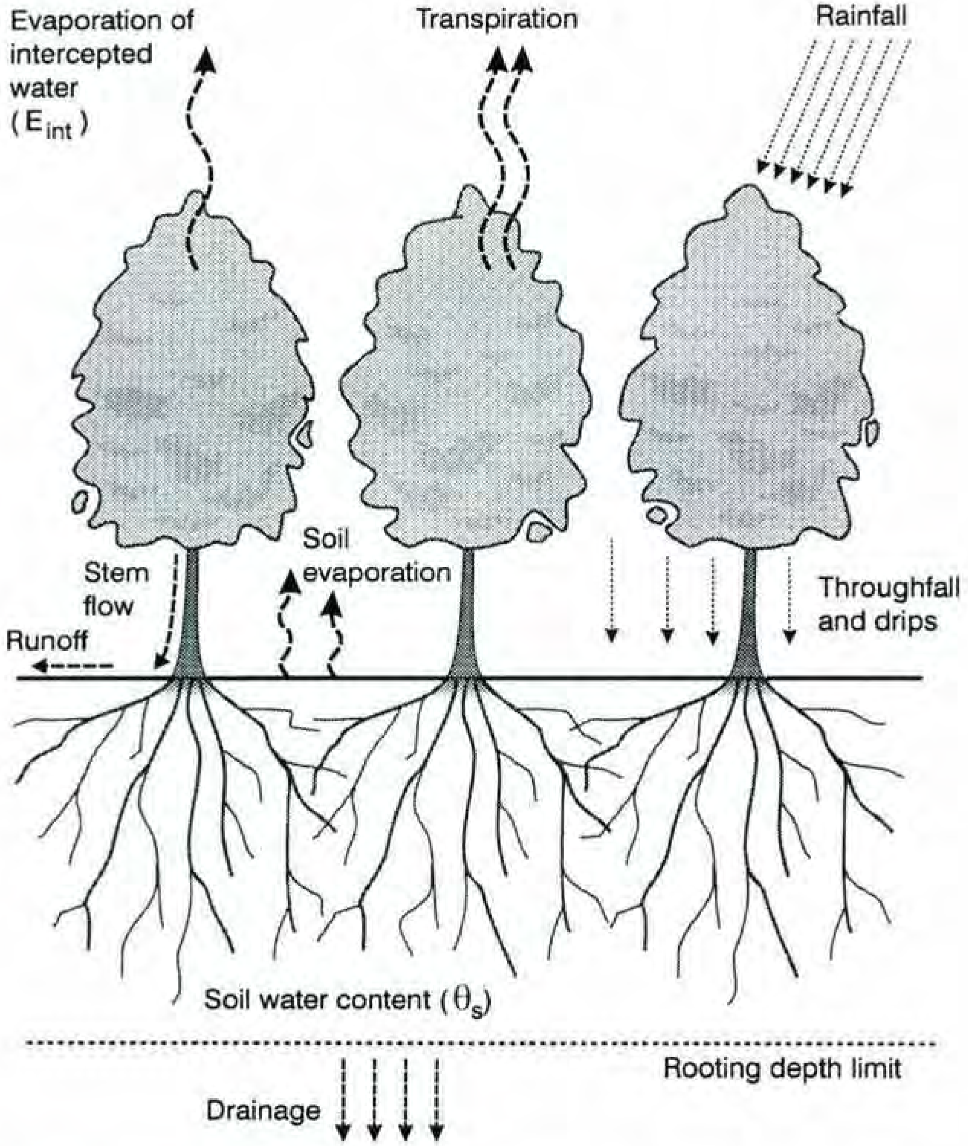


Figure 3.4 Diagrammatic representation of the hydrologic equation (equation 13)

as well as soil water-holding characteristics, will determine how much water can by used by the trees. The whole question of water balance modelling is the subject of a vast literature, and cannot be summarised here. Landsberg (1986) deals with it in some detail, and the book by Hillel (1980) appears to be among the best of many possible references.

Because of the high spatial variability of rainfall, to solve the water balance for any particular plantation requires measurements of R_f made as near to the site as possible.

There have been many studies on rainfall interception and the evaporation of intercepted water, including for tropical forests (see Calder, Wright and Murdiyarso 1986; Lloyd and Marques 1988) and good models of the evaporation of intercepted water have been developed (Calder 1986; Lloyd and Marques 1988). The key parameter governing interception loss is the canopy storage capacity, which will depend on leaf area and canopy architecture. The nature of the rainfall also influences interception: if it occurs in relatively frequent, light falls, with intervening periods during which the water intercepted in the previous fall can evaporate from the canopy, interception losses will be high. Heavy falls will rapidly saturate canopy storage, after which the rain will reach the ground either as stemflow or throughfall. Throughfall may reach the ground without touching foliage, or it may take the form of foliage drip. Calder (1986) found that 21% of rainfall was lost by interception from a tropical forest in Java, while interception losses from the Amazon forest were about 9% (Shuttleworth 1988).

There appear to have been few measurements of the various components of Equation (13) as it relates to tropical plantations (as opposed to natural forests). Tropical plantations may not behave significantly differently from plantations in temperate regions, particularly after canopy closure, but it is important that the data be collected to quantify the hydrology (and all other aspects of the biophysical environment), particularly in the pre-canopy closure stages, for which there is not much information. The nature of rainfall in the tropics, and the canopy architecture of tropical plantations—including factors such as leaf size—may result in some surprises. The proportions of precipitation that are intercepted and evaporated from the canopies, or go to runoff and drainage, will vary with species, stage of development, soil type and rainfall characteristics. (It will be clear, from this brief outline, why the water balance estimates in Figure 3.1 provide no more than rough guides to the probable water balance of plantations, which must be characterised over the developmental cycle, from early development to full canopy, as well as seasonally.)

In periods without rain, Equation (13) reduces to $\Delta\theta_S = -E_t$, where E_t is the amount of water transpired over time. The rate of transpiration is dependent on the energy balance of the canopy and atmospheric transport processes, interacting with plant properties, characterised by g_S. The best known and most widely used formula for calculating transpiration from plant communities is the Penman-Monteith equation, a combination energy balance-mass transfer equation which essentially considers the canopy as a single large leaf. It is derived from the leaf (surface) energy balance equation; the derivation can be found in Landsberg (1986), Monteith and Unsworth (1990) and Jones (1992). The equation is

$$\lambda E = (s.\phi_n + \rho\, c_p\, g_a D) / (s + \gamma\,(g_a/g_c)) \qquad (14)$$

where s is the slope of the saturation vapour pressure/temperature curve at air temperature, g_a is the canopy boundary layer conductance and g_c is the canopy conductance ($g_c = 1/(r_a + r_s)$), determined, to a large extent, by the stomatal conductance g_S (see later).

Although Equation (14) looks, at first sight, as if it requires a large number of parameter values, in fact it requires a measure or estimate of ϕ_n, an estimate of vapour pressure deficit (D) from conventional meteorological measurements, and estimates of g_c and g_s. As written here the equation calculates the flux of water vapour in energy units (λE = W m^{-2}); the conductances (s m^{-1}) contain the dimension of time. Therefore ϕ_n must be in W m^{-2}. R. Leuning (pers. comm.) has shown that simply dividing the daily energy income by the number of seconds in a day (between sunrise and sunset) provides an estimate of ϕ_n which, when used in Equation (14), gives results that are not significantly worse than those obtained by the more rigorous procedure of calculating hourly values of λE from continuous measurements, and summing them. Similarly, daily average values of D, and of the conductance values, provide good results. Clearly errors will increase as the time period of the averaging procedure increases: better results will be obtained for a month by summing daily totals than by using mean daily values, but mean daily values will, nevertheless, provide useful results.

Equation (14) is not sensitive to g_a (Raupach and Finnigan 1988), so any reasonable estimate will suffice. For example Landsberg (1986) cites results which lead to $g_a \approx u(h)/10$, where u(h) is the wind speed at the top of the canopy. Canopy conductance is often estimated as the sum of the stomatal conductances for all the foliage in the canopy, i.e $g_c = \Sigma\, g_s\, L^*$ (see, for example, Grace et al. 1982). However, Raupach and Finnigan (1988) have demonstrated that this is not equal to the bulk canopy conductance because g_c includes an aerodynamic component and is therefore not a purely physiological parameter, and also because the physiological conductance does not reflect contributions to canopy evaporation from sources such as the soil and free (intercepted) water on the foliage. It would be of particular value, in research on tropical plantations, if values of g_c were derived using experimentally-determined values of E and solving Equation (14) for g_c, i.e.

$$1/g_c = (1/\lambda E\gamma)\,(s\phi_n/g_a + \rho\, c_p\, D) - s/\gamma g_a \qquad (15)$$

As an example, assume that measurements over a period of weeks indicated that for a particular plantation E_t = 4 mm day^{-1}. We will take g_a = 0.2 m s^{-1}—a typical value for tree canopies (see Kelliher, Leuning and Schulze 1993), average ϕ_n = 13.9 MJ day^{-1}, i.e. 13.9×10^6 J (see earlier calculation) and average air temperature = 28°C, with relative humidity 80%, giving D = 0.76 kPa. Since 4 mm day^{-1} is equivalent to 4 kg m^{-2}, $\lambda E = 4 \times 2.44 \times 10^6$ J m^{-2}. Inserting these values into Equation (15), with appropriate values for the parameters ($s \approx 0.22$ kPa °C^{-1}; $\gamma =$ 0.064 kPa °C^{-1}; $\rho = 1.2$ kg m^{-3} and $c_p = 1 \times 10^3$ J kg^{-1}, gives $1/g_c \approx 70$ s m^{-1}, i.e. $g_c \approx 0.014$ m s^{-1}. If such values can be obtained for a range of plantation types and situations it will become possible to use the Penman-Monteith equation in a diagnostic and predictive sense in relation to tropical plantations.

Note that the assumption generally underlying calculations such as the one above is that the plant community has a full canopy. The calculations would be valid for incomplete tree canopies, but the results would then reflect evapotranspiration rates from the soil and weeds, grass or crops between tree rows, as well as transpiration from the trees, and the resulting values of g_c will be very difficult to interpret. Separating the contributions of the various components of the canopy to evapotranspiration will require careful research.

Equation (14) is usually applied to canopies, but it can be applied at leaf level, when the conductance values used are those relevant to the leaves (see Butler 1976).

One other aspect of the hydrologic balance that requires mention is the whole area of tree–water relations. The field is vast and covered by an enormous literature (see, for example, Slatyer 1967; Lange, Kappen and Schulze 1976 and the treatment in Landsberg 1986).The general point that needs to be made here is that plant water status at any time depends on the balance between the rate of water uptake, driven by transpiration and, when water in the soil is limited, governed by the plant's capacity to extract the water available. Plant water status is highly dynamic, which must be appreciated when attempts are made to interpret plant water potential measurements (Ψ_1)—made, for example, with a pressure 'bomb'. Among the most useful data that can be collected, as a basis for evaluating the effects of water status on growth, are pre-dawn water potential measurements, when Ψ_1 can be assumed to be in equilibrium with the integrated water potential in the root zone. Myers (1988) has shown that simple integration of such data in terms of time provides a 'stress index' that correlates well to various measures of tree growth (Benson, Myers and Raison 1992). This approach deserves further exploration. Research should also focus on calculated soil water balances, and attempts made to identify the points at which root-zone soil water content checks plant growth. Again this is an approach that has been used with many plant communities (mainly crops, with some work on trees), but which warrants detailed attention in the tropics.

Plantation Productivity

The traditional approach to estimating forest productivity for forest operations is the use of site indices and yield tables, acknowledged to be circular, since yield tables are based on site indices, derived from measurements made on trees grown on particular sites. The resulting models cannot be used for extrapolation, except within areas where they were derived, and where the soils and climate are similar to those where growth measurements were made. Nor can they be used to evaluate the possible impact of change, whether it be climate change or changes in management practices or the effects of insect attack or disease. The question is, however, whether there is anything better.

The answer, at present, is almost certainly 'no', particularly in view of the vast experience with site indexes and yield tables built up around the world. However, it should be possible to develop process-based, mechanistic models that overcome the shortcomings of the traditional system. Such (research) models already exist in various forms (e.g. McMurtrie, Rook and Kelliher 1990; Running and Coughlan 1988; Running and Gower 1991), but they are complex and have not been adapted for use by managers and decision makers. The model discussed in this paper is soundly-based physiologically and can be readily parameterised and used by those concerned with estimating forest or plantation growth rates and yields. It is discussed in considerable detail by Landsberg et al. (1996), where the physiological basis of the model is described.[1]

Called the epsilon (ε) model, it derives from an analysis by Monteith (1977), in which he demonstrated that dry matter production by plant communities is linearly related to absorbed short-wave radiant energy ($\phi_{s.abs}$):

$$\Delta P = \varepsilon . \phi_{s.abs} \Delta t \qquad (16)$$

where ΔP is the net primary (above-ground) production produced by the absorption of $\phi_{s.abs}$ over time interval Δt. (I will omit the Δt from now on). We have to recognise that the proportion of the carbon products of photosynthesis allocated by trees to their component parts (roots, stems, branches, leaves; see below) is not constant, varying not only with age but also with growing conditions, so concentration on above-ground growth, and ignoring roots, will lead to uncertainties and errors in prediction. However, for present purposes this uncertainty will be accepted.

Net primary production (NPP) is defined as

$$P_p = G_p - R_a \qquad (17)$$

where G_p (gross primary production) is the net photosynthesis of the leaves of the trees and R_a is the autotrophic respiration of the stems, branches and roots integrated over an appropriate period of time. NPP is the increase in dry mass of the living trees over the period of integration. If NPP is estimated from sequential measurements, or sampling, over an interval $\Delta t = t_2 - t_1$, then NPP is the change in standing biomass (ΔW) plus the material produced after t_1 which is lost as litterfall before t_2.

The linearity of the relationship between $\phi_{s.abs}$ and P has been demonstrated for trees in plantations by a number of scientists (e.g. Linder 1985; Beadle and Inions 1990) and has been applied to tropical forests by Saldarriaga and Luxmoore

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[1] Since this paper was drafted, a new model, based on the principles outlined here, has been produced by Landsberg and Waring (1997). Called 3-PG, the model shows promise of meeting many of the requirements of forest managers for a tool with which growth and yield can be calculated from weather data and some basic information about soils. 3-PG includes a solution to the problem of carbon allocation to foliage, stems and roots and produces, as output, stem number and stand (wood) volume.

(1991). Clearly, if Equation (17) is to be used for predictive purposes, the value of ε is of crucial importance. It has been found to vary widely (see Landsberg et al. 1996). For unconstrained growth—where nutrition, temperature and water are not limiting—it appears that a value for ε of about 1.8 – 2 g dry matter/MJ PAR will be appropriate for plantations. The apparent value, when growth is limited for some reason, may be considerably lower if the efficiency with which the canopy can use the absorbed energy is reduced by the limiting factor. For example, a canopy under serious water stress, which causes stomatal closure, will continue to absorb energy but photosynthesis may be effectively zero. Similarly, if leaves are low in nutrients their photosynthetic capacity will be reduced.

These effects are accounted for by writing Equation (17) in the form

$$P = \varepsilon . \phi_{s.abs} . m_w . m_n \qquad (18)$$

where m_w and m_n are dimensionless modifiers for water and nutrition taking values between 0 and 1 (Landsberg 1986, p.172). In temperate regions temperature will also cause reductions in growth. These values have to be established by research, for example using as baseline data growth measurements (dry matter estimates) from plots where every effort has been made to eliminate limiting factors, so that $m_i = 1$. They are applied across the interval Δt. Given appropriate values (e.g. $m_n = f$ (cation exchange capacity, N-mineralisation potential); $m_w = f$ (site water status)) the model can be used to estimate probable growth rates, and hence yields, on any site for which ϕ_s data are available, and water balance calculations can be made. This has the additional advantage that the probability of drought (for example), and its effects, can be incorporated into site assessment. Ironically, in view of the large amount of research on forest and plantation nutrition over the years, accounting for the effects of nutrition on radiation conversion efficiency is a largely unsolved problem. We have vast amounts of empirical information about growth in relation to nutrition in particular situations, but appear to have no theoretical basis for calculating the influence of nutrients on tree growth in soils with nutrient status specified in conventional terms. Progress is being made in modelling the uptake and utilisation of nitrogen (see, for example, McMurtrie 1985) but models of the type developed by McMurtrie are not suitable for practical application, and little progress has been made in relation to phosphorus and the other essential nutrients. It seems that, for the foreseeable future, we will have to rely for modifier values on empirical relationships established in projects designed for the purposes of testing and parameterising the model(s). At least this approach may lead to more rapid progress than has been made by an endless succession of conventional nutrition trials.

To establish values for ε, growth measurements should be made at least once a month (unless the trees are deciduous; there is no point in measuring growth on leafless trees). Annual measurements do not provide enough information: periods of water stress may persist for days or weeks, and can be identified if growth measurements are sufficiently frequent. Nutritional effects may be identified over longer periods than the effects of water stress. Frequent growth measurements, particularly if maintained over long periods, provide a considerable amount of valuable information, and frequent analyses to determine foliage nutrient concentrations should also be done, if possible, since these fluctuate in relation to rates of supply from the soil and internal retranslocation in response to growth patterns.

The procedures for estimating $\phi_{s.abs}$ have been discussed earlier. A relatively detailed description of the estimation of ε and the application of the model is provided by Landsberg and Wright (1989).

The ε-model has the potential to overcome the limitations of site index and yield table methods because it is based on sound physiological processes (energy absorption and photosynthesis) and provides a means of incorporating nutrition and water status into productivity models. However, those concerned with estimating plantation productivity will note that the model is described in terms of dry matter production on a unit ground area basis, and point out that this is not a parameter of great interest to managers or those concerned with the estimation of commercial yields.

There are two possible solutions to this problem:

- ε can be established in terms of conventional volume growth, which can be converted into information about economic timber yields on the basis of stand density and tree height. This has advantages from the practical point of view, but has the major disadvantage that the results cannot be compared to other dry matter production research; the model is reduced to a level of pragmatic empiricism that greatly reduces its value, although useful information can still be obtained;
- dry matter can be partitioned between stems, branches and leaves on the basis of allometric ratios. The commonly established relationship between diameter at breast height (d_b) and foliage mass mentioned in the section on 'Canopy Architecture' is an allometric ratio, and statistically-strong relationships of the form

$$w_j = c_j d_b^n \qquad (19)$$

where c_j is an empirical constant, can normally be established for any tree component. Given such relationships they can be used to partition total above-ground (standing) dry mass, which consists of foliage (w_f), branches (w_{br}) and stems (w_{st}):

$$W(t) = w_f + w_{br} + w_{st} \qquad (20)$$

Although the values of c_j and n will vary with species and growing conditions, they appear to be relatively conservative. They are obtained by destructive sampling of a number of trees, and their establishment for tropical plantations is a matter of some importance. Given the mass of material in stems, stem number and height provides the information needed for commercial purposes. More detailed analysis could include the use of standard forestry stem size distribution equations (e.g. the Weibull distribution) which would allow detailed estimates of the value of the product.

Synthesis

This chapter has provided an outline of the factors of the biophysical environment that will affect the growth of plantation forests in the tropics. Since these are the same factors, operating through the same mechanisms, that affect plant communities anywhere—whether forests, mixed ecosystems or plantations—the treatment has necessarily been general, with an attempt to provide information relevant to tropical plantations, or at least tropical forests, wherever possible. Emphasis throughout has been on processes and quantitative treatment, although I recognise that, in many cases, those working on the establishment of tropical plantations will not have sophisticated instrumentation at their disposal. Nevertheless, much can be done with simple measurements—good weather data, descriptions of canopy architecture and thorough descriptions of soil depth and physical characteristics. Destructive harvesting should be carried out wherever possible, since the mass and arrangement of foliage, and the distribution of standing biomass, are not only the most important determinants of the way plantations will interact with the atmospheric environment, but are also, as the last section shows, themselves the end results of the interactions. Experiments should therefore include in their design allowance for intermittent destructive harvests; these will be of immense value in nutritional studies as well as for estimating dry matter production in relation to radiant energy.

Radiant energy should, wherever possible, be measured. It can, if necessary, be estimated from measurements of sunshine hours (e.g. Stigter 1980) but on-site or at least regional measurements are of great value. Similarly, net radiation should be measured over plantations wherever possible although it can be calculated, as described in the section on 'Radiation absorption and energy balance', to provide the values needed to calculate transpiration. Since the coefficients in the empirical relationships are conservative the errors will not be large.

Hydrologic measurements are relatively simple, and the hydrology of plantations throughout their growth cycle should be characterised. There are concerns, in various parts of the world, arising from the apparent tendency of deep-rooted trees such as *Eucalyptus* to lower ground water tables and disrupt regional hydrology. These concerns can only be confirmed or dismissed on the basis of good quality, rigorous measurements; unsupported assertions do not provide a basis for decisions that may have considerable effects on regional ecology and human welfare. The equations for calculating transpiration should be tested and parameterised on the basis of water balance experiments, so that plantation water use can be calculated with confidence for situations where there are no measurements.[2]

The last section of the chapter provides an outline of a simple but soundly-based model for estimating plantation productivity. The point is often made that such models cannot compete with the traditional approach of site indices and yield tables, and this is currently true. However, if the effort expended on the development of these traditional, non-transportable methods of growth and yield estimation was directed towards the development and parameterisation of simple process-based models, I have no hesitation in predicting that it would not be many years before we would have available methods of yield estimation which would be much more flexible and informative than the traditional methods. The methods advocated require information about soil physical properties and fertility that could be used to calculate the radiation utilisation modifiers in eqn (18). As the development of tropical plantations gains impetus the opportunity to develop these models should not be missed.

Acknowledgments

It was not easy to produce a description of turbulent transfer, with a minimum number of equations, at the level appropriate for this chapter. That section owes a great deal to help from Dr John Finnigan.

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[2] Note, in relation to the question of water use by *Eucalyptus* species, that studies reviewed by Calder (1992) indicate that annual evaporative losses will increase markedly from land previously occupied by agricultural crops if forests or plantations of *Eucalyptus* or any other tree species are established; but there are unlikely to be large changes in water use if *Eucalyptus*, or any other tree species, are established on land previously occupied by forest or degraded forest.

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4

Soils of the Tropics and Their Management for Plantation Forestry

R. Lal

Abstract

In the tropics the per capita arable land area is decreasing because soil resources are limited and prone to degradation, and population is rapidly increasing. The number of countries in the tropics with an arable land area of less than 0.1 ha per capita was 8 in 1990 and will be 45 in 2025. Predominant soils of the tropics are Oxisols (22.5% of the land area in the tropics), Ultisols (10.6%), Aridisols (18.4%), Alfisols (16.3%), Entisols (10.0%) and Inceptisols (5.0%). With some exceptions (e.g. Etisols, Inceptisols, Andisols, Mollisols and Histosols), most soils have low inherent fertility and several soil-related constraints to sustained intensive cropping. Oxisols and Ultisols have generally favourable physical characteristics, but are highly acidic and have severe problems of nutrient imbalance. Alfisols and Aridisols may have favourable soil chemical and nutritional properties but are severely constrained by adverse soil physical conditions, e.g. compaction and erosion. Because land misuse and soil mismanagement cause soil degradation, appropriate land use and judicious soil and vegetation management can restore soil quality and enhance productivity. High erosion risks in the tropics, accentuated by soil erodibility and high climatic erosivity, can be partially mitigated by establishing a protective ground cover and judicious inputs of soil amendments. Runoff management through engineering structures (i.e. terraces, gabiens, chutes, drop structures etc.) also decreases risks of soil erosion. Development and management of plantation forestry in the tropics must take into account the diverse and highly variable nature of tropical soils and their responses to management systems.

PRIME SOILS of the tropics, with few constraints to intensive land use, are limited in area and unequally distributed. The prime land area per capita in most countries of the tropics, especially those in South and Southeast Asia, is decreasing because of rapidly increasing population and conversion of land to new uses. Total arable land area in the world in 1993 was estimated at 1346 million ha including 164 million ha in Africa, 124 million ha in Latin America, and 476 million ha in Asia and Oceania (FAO 1993). The number of countries in the tropics with per capita land area of < 0.1 ha was 8 in 1990 and will be 45 in the year 2025. The land area in the world under permanent crops (including plantation forestry) in 1993 was 98 million ha including 19 million ha in Africa, 19 million ha in Latin America and 35 million ha in Asia and Oceania (FAO 1993). Generally, the area under arable land use and permanent crops is increased at the expense of that under forest and woodlands (Engelman and LeRoy 1995). The land area under forest and woodlands in 1993 was 3880 million ha in the world: 678 million ha in Africa, 880 million in Latin America and 693 million ha in Asia and Oceania.

In addition to the unprecedented population pressure (Haub 1995), the availability of prime land per capita is decreasing because of soil degradation. Soil degradation is a serious global problem and is more severe now than ever before, especially in ecologically-sensitive regions of the tropics and subtropics. The global extent of soil degradation by different processes is estimated at 1094 million ha by water erosion, 548 million ha by wind erosion, 240 million ha by chemical degradation, and 83 million ha by physical degradation (Oldeman 1994). The principal causes of soil degradation are deforestation (579 million ha), overgrazing (677 million ha), agricultural activities (552 million ha), over-exploitation (133 million ha) and bio-industrial activities (23 million ha). The total area of degraded soil in different continents is estimated at 494 million ha in Africa, 849 million ha in Asia and Oceania, and 306 million ha in Latin America (Oldeman 1994). The severe problem of soil degradation in the tropics has endangered agricultural sustainability and environmental quality.

A soil's susceptibility to degradation depends on many factors including its intrinsic properties, climate, land use, and soil and vegetation management. Soil physical properties play an important role in relation to the resilience and degradation of the soil. Resilience is defined as soil's ability to recover and restore its life support processes and environmental regulatory functions (Lal 1994a). Key soil physical properties in relation to enhancing soil resilience and facilitating sustainable use of soil and water resources are soil structure, soil bulk density, total porosity and pore size distribution, water retention characteristics and available water holding capacity, and water transmission properties including infiltration capacity.

The objective of this paper is to identify the principal soils of the tropics, describe key soil physical properties, discuss soil-related constraints to plantation forestry and outline the principles of soil management.

Soils of the Tropics

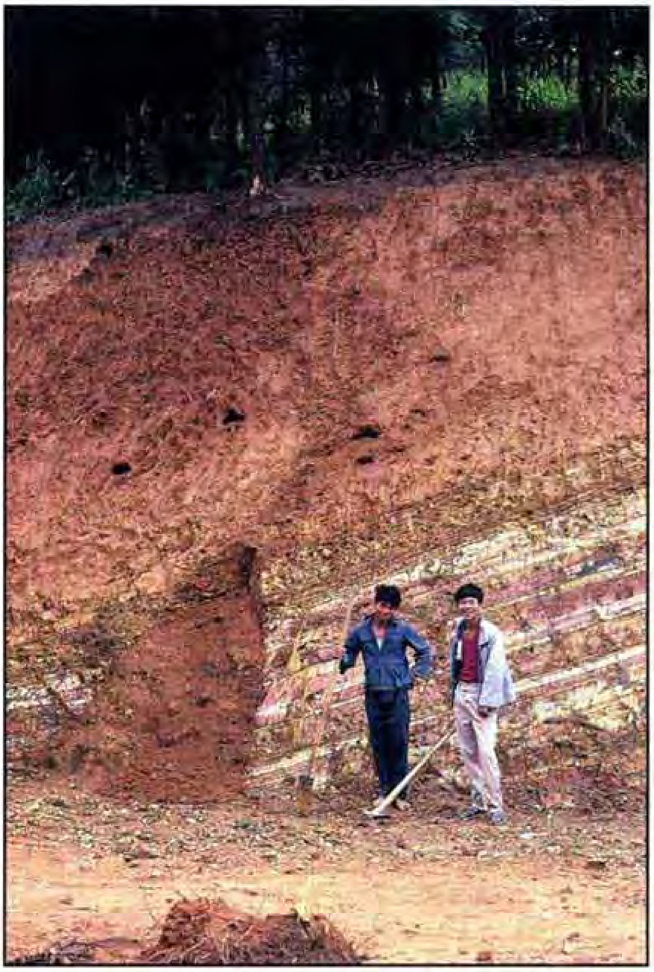
The soils of interest occur between the Tropic of Cancer and the Tropic of Capricorn. There are several soil classification systems; the description of soils in this chapter is based on Soil Taxonomy (Soil Survey Staff 1990). There are two basic assumptions of Soil Taxonomy (Smith 1963): i) soil is the result of the interaction of climate, relief and living organisms acting over time on the parent material; and ii) whenever the soils are the same, the responses that depend upon soil properties are the same. According to this system, soils are classified into phases, series, family, subgroup, great group, suborder and order. Soils of the tropics include at least 10 million phases, 5 million series, 1 million families, 1250 subgroups, 200 great groups, 45 suborders, and 11 orders (Eswaran et al. 1992). In the interest of space, this paper describes soils of the tropics at the order level, and for more detail readers are referred to Van Wambeke (1992) and Eswaran et al. (1992).

The principal soils of the tropics comprise Oxisols, Ultisols, Aridisols, Alfisols and Entisols (Table 4.1), which together cover about 75% of the total land area in the tropics. Characteristics of principal soil orders are given in detail by Soil Survey Staff (1990) and briefly described below:

Table 4.1 Principal soil orders of the tropics

Soil order	**World land area**		**Land area of the tropics**	
	(10^6 ha)	**(%)**	**(10^6 ha)**	**(%)**
Alfisols	1730	13.1	800	16.3
Aridisols	2480	18.8	900	18.4
Entisols	1090	8.2	490	10.0
Histosols	120	0.9	50	1.0
Inceptisols	1170	8.9	243	5.0
Mollisols	1130	8.6	50	1.0
Oxisols	1120	8.5	1100	22.5
Spodosols	560	4.3	6	0.1
Ultisols	730	5.6	520	10.6
Vertisols	230	1.8	200	4.1
Highlands	2810	21.3	541	11.0
Total	**13170**	**100**	**4900**	**100**

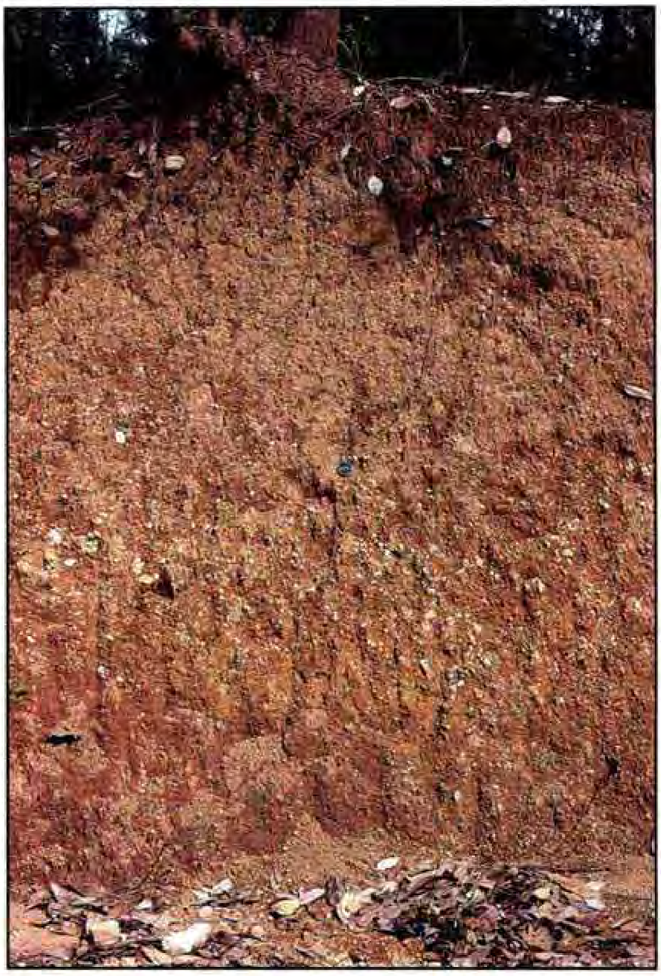
Source: Buringh 1979; Van Wambeke 1992



Deep well-structured Humic Latosol (Oxisol). Gradational acidic red clay loam profile with strong humic development in surface horizons and increasing clay with depth, developed on banded metamorphosed shales and chert. Plantation of *Cunninghamia lanceolata*. Gao Feng, Guang Xi, China. Photo: D.I. Bevege, ACIAR

Oxisols

These soils are strongly weathered, well-drained and acidic with low base saturation, and have 40% or more clay in the surface 18 cm and an oxic horizon (Soil Survey Staff 1990). An oxic horizon is a subsurface horizon characterised by: i) an effective cation exchange capacity of less than 12 cmol (+) per kg clay; ii) <1.2 times the clay content of the surface horizon (20% to 40% clay in the surface horizon); and iii) <10 % of total weatherable minerals. Oxisols have low inherent fertility and contain strongly cemented microaggregates giving them high aggregate stability. The clay fraction contains predominantly kaolinite with relatively low surface area and low charge density. Oxisols are generally formed under tropical rainforest vegetation.



Deep texture contrast (duplex) Podsolic profile, with blocky structured B horizon and lateritised mottled C horizon (Ultisol). Coarse gravel throughout. Developed on sediments and shales. A horizon hard setting sandy loam degraded by sheet erosion while under agriculture prior to reforestation with mixed *Eucalyptus* spp. Dongmen, Guang Xi, China. Photo: D.I. Bevege, ACIAR

Ultisols

These soils are also strongly weathered but less so than Oxisols, well-drained, highly leached and acidic, and contain an argillic or kandic horizon. An argillic horizon has a high clay content and is similar to an oxic horizon; the mineralogy indicates strong weathering. The high clay content of the argillic horizon may be due to: i) sedimentation; ii) illuviation; and iii) lithological discontinuities. Some weatherable minerals may occur in silt and sand fractions. The argillic horizon must have less than 35% base saturation. These soils also have low pH, and are low in inherent fertility.

Well-drained lateritic Red Earth, gradational acidic profile with increasing clay and lateritic gravel with depth, some organic accumulation in A1 horizon and bleached A2, massively structured (Ultisol). Developed on sediments. *Eucalyptus exserta* plantation. Dongmen, Guang Xi, China. Photo: D.I. Bevege, ACIAR

Alfisols

These soils are less weathered than either Oxisols or Ultisols. Similar to Ultisols, however, Alfisols also have an argillic horizon, but the base saturation is more than 35%. Most Alfisols occur in the sub-humid or semi-arid rather than humid regions These soils have favourable chemical and nutritional properties, containing weatherable minerals even in the clay fraction, but have less favourable soil physical characteristics than Ultisols and Oxisols.

Aridisols

These soils, developed in dry areas, are characterised by accumulation of calcium carbonate, gypsum and other salts in the soil profile. Water is held at less than –1.5 MPa or below the permanent wilting point for more than 9 months a year. Soil moisture stress is the major limitation to crop production. Some soils, especially when irrigated with poor quality water, are prone to salt accumulation in the root zone and to wind and water erosion.

Shallow brown forest soil, loam to clay loam gradational profile increasing clay and strengthening irregular blocky structure with depth, developed on fine grained granodiorite (Alfisol). *Pinus caribaea* plantation. Cathu, Queensland, Australia. Photo: D.I. Bevege, ACIAR

Inceptisols

These are relatively young soils and, therefore, less weathered. They are developed on recent geomorphic surfaces, e.g. alluvial deposits. Because of a large proportion of weatherable minerals, these soils have high inherent fertility. Inceptisols occupy relatively large land areas.

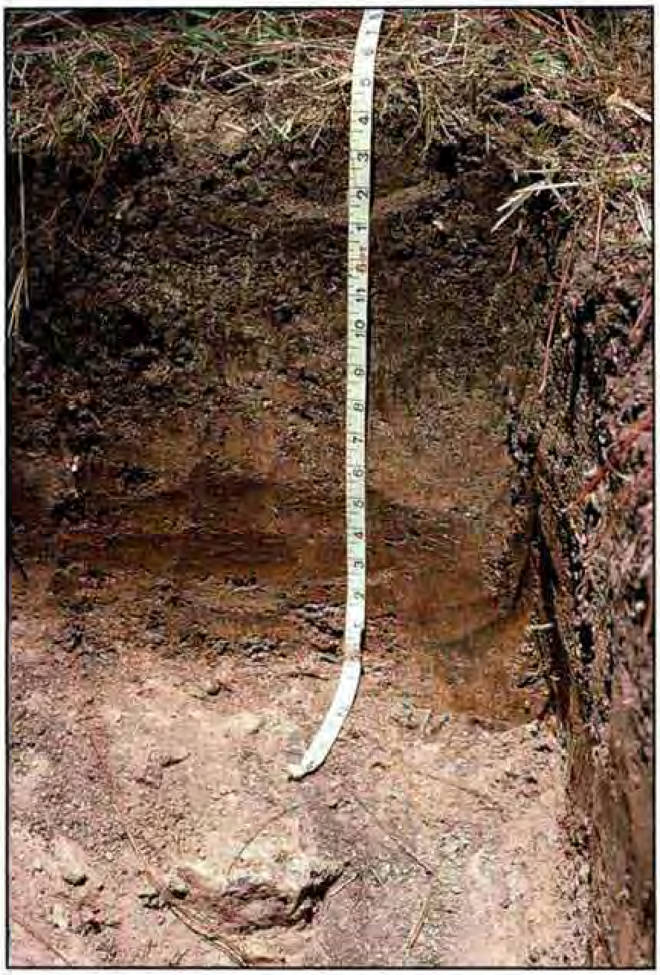
Shallow grey-brown stony loam (Lithosol) with organic accumulation and humification in surface horizon, developed on colluvium derived from hornfels (Inceptisol). *Pinus elliottii* and *P. caribaea* plantations. Zhi Po, Guang Xi, China. Photo: D.I. Bevege, ACIAR

Entisols

Entisols are also less developed and often lack distinct horizons, e.g. recent alluvial or colluvial deposits. Some soils on flood plains are highly productive and suitable for intensive agriculture.

Spodosols

These soils are characterised by a subsurface illuvial horizon with relatively high organic matter content. The surface or eluvial horizon is usually leached and is often light in colour.



Shallow prairie soil; uniform nigrescent clay with prismatic structured melanised horizon, developed on basalt in a seasonal rainfall environment, restricted drainage when wet, droughty when dry (Mollisol). Reaction acidic tending alkaline with depth. Plantation of *Pinus caribaea*. Koro, Fiji. Photo: D.I. Bevege, ACIAR

Vertisols

These dark, heavy-textured, montmorillonitic soils are formed in the semi-arid tropics. Vertisols are calcareous and have high shrink-swell properties, and develop deep and wide cracks on drying. Intensive use of these soils is severely constrained by their unfavourable physical properties and difficulties of tillage and traffic when wet. The range of soil moisture content at which soils can be managed is rather narrow. Poor trafficability, susceptibility to severe water erosion and poor drainage during the rainy season are major soil management problems

Histosols

These soils have relatively high soil organic matter content, and therefore with good water management they can be highly productive. Histosols have favourable soil physical properties and high inherent fertility.

Distribution of principal soil orders in different climatic regimes is shown in Table 4.2 and Figure 4.1. Predominant soils of the humid tropics are Oxisols, Ultisols and Alfisols comprising about 78% of the total land area. Major soils of the sub-humid and semi-arid tropics are Oxisols, Alfisols and Inceptisols comprising about 75% of the region (Fig. 4.2). In contrast, predominant soils of the dry and arid tropics are Aridisols and Psamments comprising about 81% of the total land area (Fig. 4.3).

Soils of the tropics are highly variable even over short distances (Prasad and Gupta 1990); this is attributed to several factors including vegetation (Demattê and Demattê 1993), tree species (Kang and Moormann 1977), termite activity (Kang 1977) and parent material.

Table 4.2 Distribution of the principal soils of the tropics according to moisture regimes (Sanchez 1976)

Soil order	Humid tropics (10^6 ha)	Sub-humid and semi-arid tropics (10^6 ha)	Dry and arid tropics (10^6 ha)	Total (10^6 ha)	Percent of the tropics
Oxisols, Ultisols, Alfisols	920	1540	51	2515	51
Psamments and lithic group	80	272	482	834	17
Aridisols	0	103	582	685	14
Alluvial (Aquepts, Fluvents)	146	192	28	366	8
Vertisols, Mollisols	24	174	93	291	6
Andepts, Tropepts	5	122	70	207	4
Total area	1175	2403	1316	4900	100
Percent of the tropics	24	49	27	100	

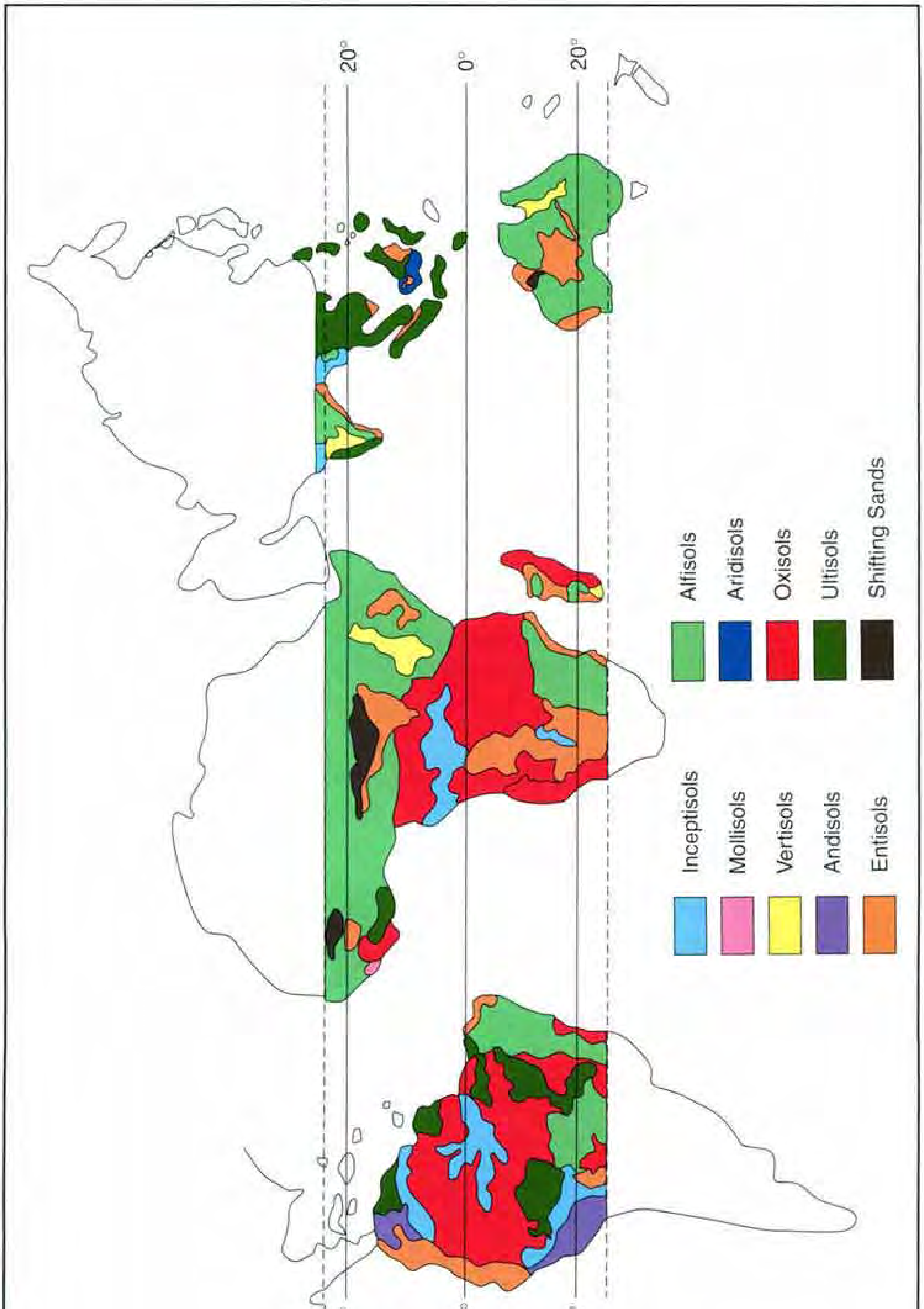


Figure 4.1 Principal soils of the arid tropics (redrawn from Dregne 1976; Eswaran 1993)

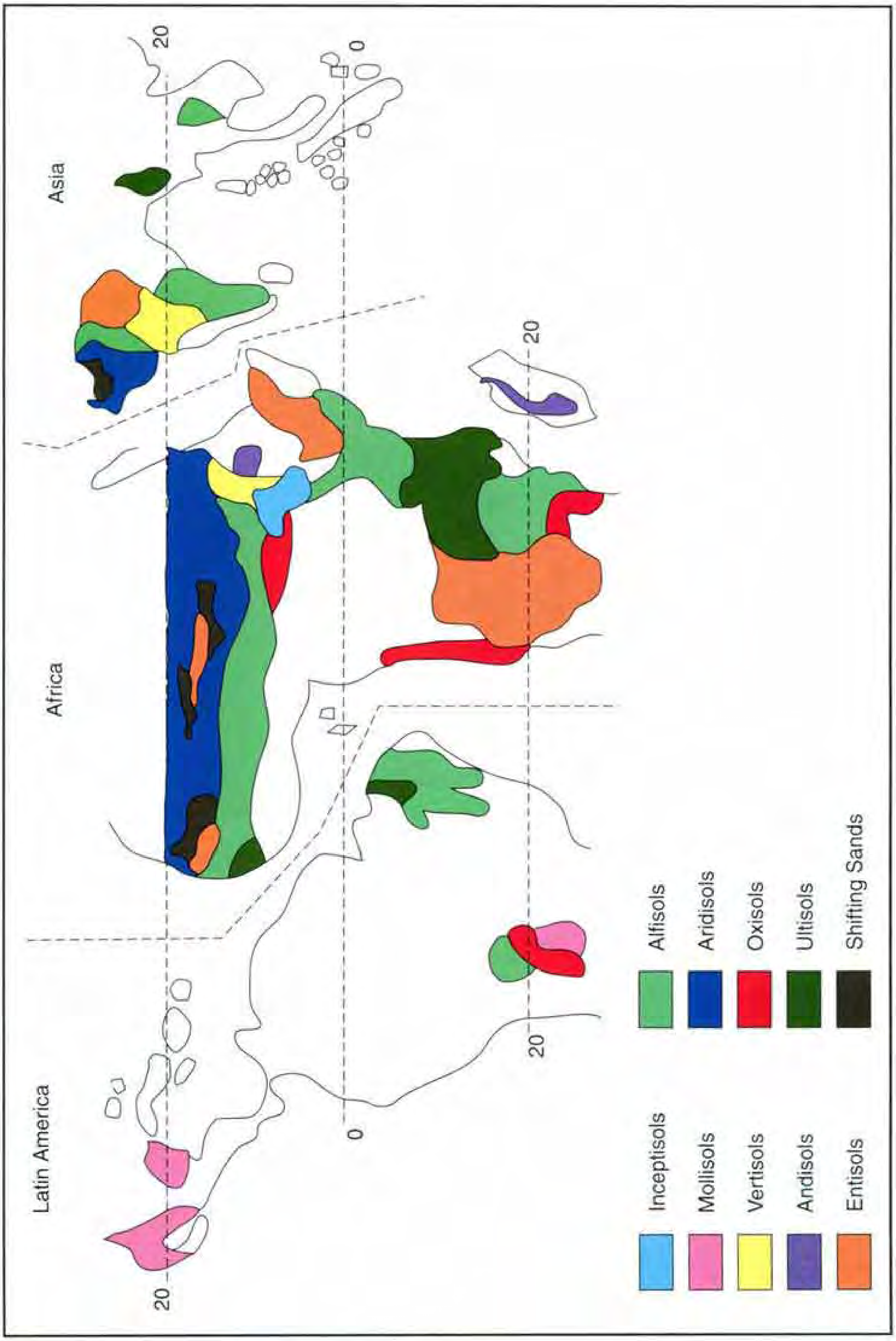


Figure 4.2 Principal soils of the semiarid tropics (redrawn from Eswaran 1993)

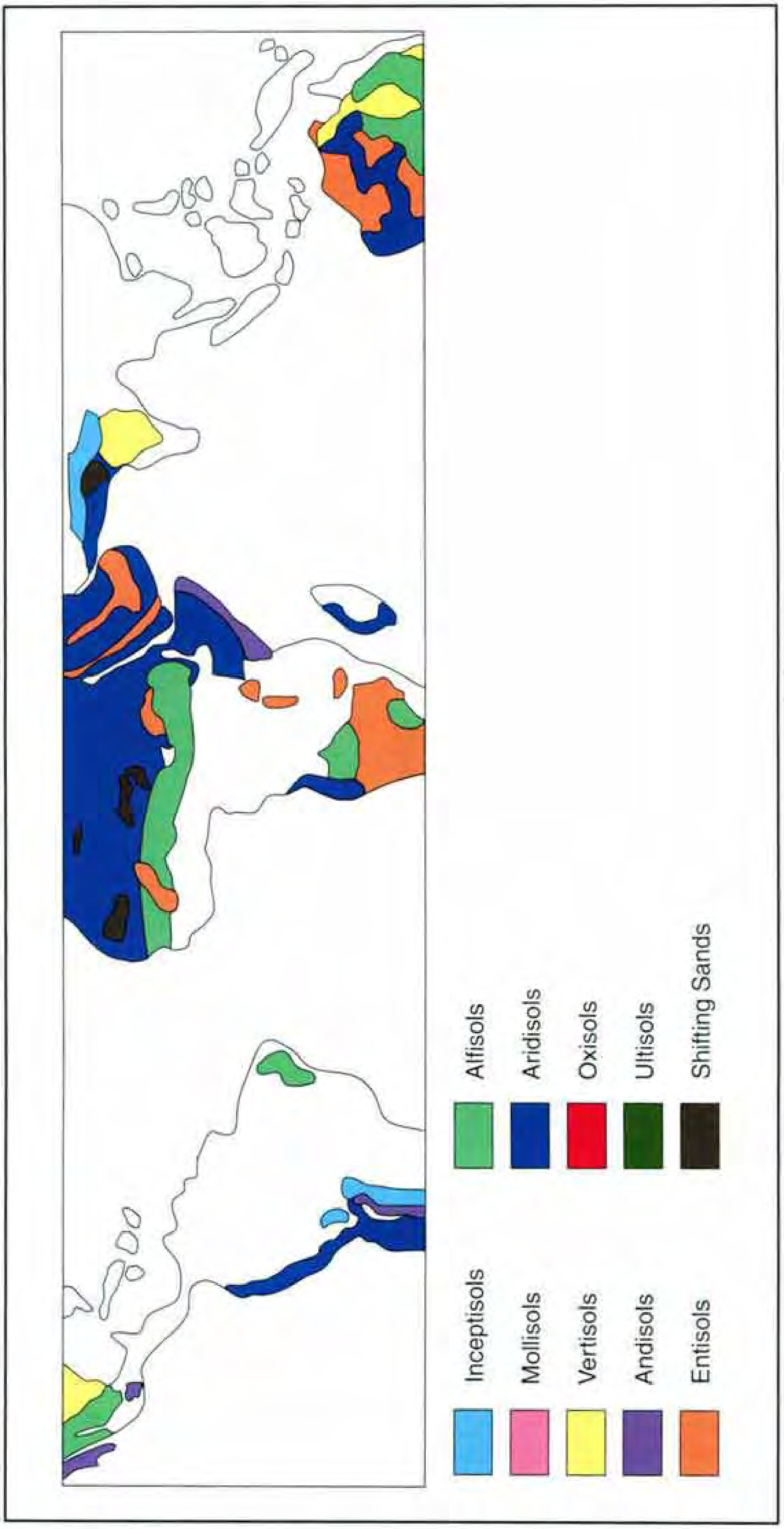


Figure 4.3 Principal soils of the arid tropics (redrawn from Eswaran 1993; El-Swaify et al. 1984)

Soil Requirements for Plantation Forestry

Some general soil-related constraints to intensive use of soils of the tropics are identified in Table 4.3. These are based on soil characteristics, moisture regime and interaction with predominant climatic factors. Soil and site-specific constraints have to be identified through detailed soil survey and soil capability classification. Using a similar approach on a regional basis, Sanchez and Salinas (1981) estimated that out of the total land area of 1493 million ha in tropical America (between 23°N and 23°S), the area affected by particular constraints is: low available water capacity—42%, high soil erosion hazard—36%, waterlogging and anaerobiosis—20%, susceptibility to compaction—11%, and risks of laterisation—8%.

Table 4.3 Soil-related constraints for plantation forestry in the tropics (Stewart et al. 1991)

Soil order	Inherent soil fertility	P availability	Erosion	Compaction/ crusting	Trafficability
Oxisol	3	3	2	2	1
Ultisols	3	3	2	2	1
Inceptisols	1	1	3	2	2
Entisols	1	1	3	2	2
Alfisols	2	1	3	3	3
Aridisols	2	1	3	3	1
Vertisols	2	2	3	3	3

3 represents severe constraint; 2 moderate constraint; and 1 slight constraint.

Sanchez and Salinas (1981), Stewart et al. (1991) and others have shown that Oxisols and Ultisols have generally favourable soil physical characteristics but are highly acidic (pH range of 4.5 to 5.5), may contain toxic concentrations of Al and Mn, are low in available P, and are low in major plant nutrients (e.g. N, P, K, Ca, Mg). Tree growth in these soils, therefore, is often correlated with the nutrient availability. In West Bengal, India, Singh et al. (1990) observed that height and growth of teak (*Tectona grandis*) was affected by soil contents of N, CEC, and exchangeable Ca. Judicious use of chemical fertilizers and amendments and choice of appropriate tree species is essential for successful plantation establishment on these soils. In contrast, Alfisols have relatively favourable soil chemical properties but are severely constrained by adverse soil physical conditions such as susceptibility to crusting, compaction and accelerated erosion (Lal 1986). Management of soil compaction and erosion are principal considerations for sustainable use. Most Inceptisols, Entisols and Histosols are highly productive soils, and have favourable soil physical and chemical properties. Judicious management involving science-based inputs can lead to high productivity and sustainable use. Aridisols are highly prone to crusting and compaction, and are susceptible to drought (Beek et al. 1980). Water deficit is the principal constraint to forestry plantations on these soils. Major constraints of Vertisols are difficult trafficability during the wet season, and drought stress and intensive cracking during the dry season. In addition to limitations of soil wetness, Vertisols are also prone to accelerated erosion. Large and deep networks of cracks can dissect the feeder roots and hinder water and nutrient absorption (Beek et al. 1980). Salt accumulation causing salinisation and sodication can also be constraints in Aridisols and Vertisols (Gupta and Abrol 1990).

Improper land use and soil mismanagement — be it in arable, pastoral or silvicultural landuse systems — can cause fertility depletion and structural degradation (see Chapters 10 and 11). For example, severe soil erosion has been observed under plantation forestry in Kenya and Trinidad (Bell 1973). Depletion of soil organic matter has been reported under teak vis-a-vis natural forest in Senegal (Maheut and Dommergues 1960) and India (Jose and Koshy 1972). Soil compaction can also be a problem, especially under the second rotation (Lundgren 1978), and during drought periods. Most plantations require well-drained soil conditions, and even temporary flooding or inundation can cause adverse effects on growth (Boomsma and Hunter 1987). In Manaus, Brazil, Mori and Becker (1991) observed that flooding of Lecythidaceae (Brazil nut) increased the incidence of mortality, leaf fall, insect attack and poor growth.

With proper land use and judicious soil and vegetation management, however, afforestation and silvicultural land use can restore soil quality and enhance productivity. Soil disturbance and vehicular traffic are usually minimal, and there is a continuous canopy cover along with leaf litter and other biomass on the soil surface that protect soil against degrading processes. Among examples of successful silvicultural projects in the tropics are the Inga plantations in Ecuador (Bishop 1983), plantation crops in East Africa (Lazier et al. 1983; Dover and Talbot 1987) and the Pulpwood Project in the Philippines (Spears 1987). While increasing economic returns, these systems also improved soil properties and enhanced soil quality.

Physical Properties of Major Soils of the Tropics

Significant soil physical properties which influence seedling establishment and tree growth are: i) soil structure; ii) soil water; iii) soil temperature; and iv) aeration. These properties are themselves affected by tree growth. Critical level(s) of these properties, beyond which tree growth is adversely affected, are not known for most soils of the tropics. Further, information on management of soil physical properties for tree growth in the tropics is scanty.

Oxisols and Ultisols

In general, Oxisols are well structured soils (Trapneli and Webster 1986) with a high proportion of microaggregates (0.01 to 0.2 mm size) stable to slaking and moderate traffic. Consequently most Oxisols, although clayey in texture, behave like fine sand in terms of moisture retention and transmission properties. Equilibrium infiltration rate and saturated hydraulic conductivity of these soils can be extremely rapid, ranging from 5 to 50 cm hr^{-1}. Continuous cultivation and vehicular traffic, however, can lead to structural degradation resulting in crusting, compaction, low infiltration rate, high runoff rate and accelerated soil erosion. The water retention capacity of Oxisols is influenced by clay and organic matter contents at high potential (e.g. field capacity) and clay content at low potential (e.g. permanent wilting point). Van Wambeke (1992) reported the following relationships between soil textural pattern and water retention (Equations 1 and 2):

$$\Theta_{pwp} = 11.2 + 275 \text{ clay } (\%) \qquad (1)$$

$$\Theta_{awc} = 7.5 + 0.7 \text{ fine silt } (\%) \qquad (2)$$

where Θ_{pwp} is the percent moisture content on volumetric basis, and Θ_{awc} is the percent moisture content held between 10 and 1500 kPa suctions.

Alfisols

In contrast to Oxisols, most Alfisols have a light-textured surface horizon often containing less than 20% clay. Furthermore, most Alfisols in the sub-humid and semi-arid tropics have a low silt fraction, are weakly structured and extremely susceptible to slaking, crusting and compaction. Because of predominantly low-activity clay (e.g. kaolinite and illite) and low soil organic matter content, most Alfisols are also prone to hard-setting, i.e. hardening of soils into a structureless mass upon drying. Ley et al. (1989) and Mullins et al. (1990) described hard-setting processes involving the following mechanisms: i) slumping or slaking following a quick wetting; ii) shrinkage upon drying; and iii) increase in strength due to bonding and close-packing arrangement.

Most Alfisols in West Africa are characterised by a coarse-textured surface horizon underlain by a clayey or argillic horizon containing a variable concentration of quartz or concretionary gravels. Under natural vegetation, most Alfisols (and Ultisols) have low soil bulk density (about 1.0 t m^{-3} or less), especially in regions characterised by high activity of soil fauna, e.g. earthworms and termites. However, soil bulk density can quickly increase with heavy mechanised traffic. The rate of increase of bulk density is rapid in soils containing little organic matter and predominantly low-activity clays. Soil bulk density can increase from 0.8 t m^{-3} under native vegetation cover to 1.4 t m^{-3} with mechanised farm operations. Such a large increase in soil bulk density following deforestation was observed in West

Africa by Lal and Cummings (1979), Hulugalle et al. (1984) and Ghuman and Lal (1991); and in the Upper Amazon region by Alegre et al. (1986). The data in Table 4 are an example of a large increase in soil bulk density following deforestation. In this case, soil bulk density increased by a factor of two regardless of the method of deforestation. The reason for low soil bulk density under forest cover is the extremely high activity of earthworms, termites and other soil fauna. The soil under forest cover feels spongy when walked over, and is covered with a 3 to 5 cm thick layer of worm casts. There is also intense activity of termites and other soil fauna. Deforestation changes soil temperature and moisture regimes, decreases food availability and diversity, disturbs the habitat, and drastically lowers soil biotic activity. Consequently, soil bulk density increases. The data on penetration resistance are in accord with those of bulk density (Table 4.4). These measurements, before and after deforestation, were made during the dry season when soil moisture content was low. Following deforestation, the soil was prone to hardsetting, high strength and high resistance (Ley et al. 1989).

Table 4.4 Soil bulk density and penetration resistance of the 0–5 cm horizon of an Alfisol in western Nigeria and the effect of deforestation

Deforestation treatment	Before deforestation		One year after deforestation	
	Bulk density ($t\ m^{-3}$)	Penetration resistance (kPa)	Bulk density ($t\ m^{-3}$)	Penetration resistance (kPa)
Manual	0.73	44	1.46	170
Shear blade	0.81	30	1.38	144
Tree pusher/ root rake	0.69	30	1.45	132
Traditional	0.69	17	1.16	121
LSD (.05)	NS	NS	0.01	20

Development of a crust or surface seal is another major physical constraint in soils exposed to raindrop impact and rapid drying following deforestation. The crust is often 1 to 5 mm thick, and has extremely slow permeability to air and water. A high fraction of water-dispersible clay, low organic matter content, and lack of or low level of swell-shrink properties lead to formation of crust. FAO (1979) proposed an index of crusting related to texture and organic matter content (Equation 3):

$$I_c = (1.5\ FS + 0.5\ CS)/(\ C + (10 \times SOC)) \qquad (3)$$

where I_c is the index of crusting, FS is fine silt percent, CS is coarse silt percent, C is clay percent, and SOC is organic carbon percent. It is primarily the low clay and organic carbon content of these soils that lead to crusting.

Increased soil bulk density, due to loss of organic matter, reduced soil biodiversity and raindrop impact, results in decreased macroporosity and reduced infiltration capacity (Lal and Cummings 1979; Ghuman et al. 1991). The magnitude of decline in infiltration capacity depends on antecedent conditions, management and soil biodiversity (Lal 1993). Soil and tree management systems that enhance activity of soil fauna also maintain high infiltration capacity (Lavelle et al. 1992).

Soil moisture retention characteristics of Alfisols and Ultisols in west Africa indicate low available water-holding capacity (Lal 1993). The high energy soil moisture characteristics of these soils show that most macropores drain at a matric potential of about 50 cm of water or 5.0 kPa. Furthermore, there is no difference in soil moisture retention between 0.1 MPa and 1.5 MPa matric potential. The permanent wilting point for most of these coarse-textured soils with clay content <20% and containing kaolinitic clay may well be between 0.1 MPa and 0.2 MPa matric potential. The available water holding capacity of most soils ranges from 3 to 5 cm for the upper 50 cm depth. Therefore, trees may suffer from drought even during the rainy season whenever the duration of a rainfree period is more than 10 days. Deep rooting with a well developed tap root system is an important characteristic of successfully adapted plantation species in these soils.

Susceptibility to drought stress is exacerbated by weak structural characteristics, and rapid deterioration of aggregates due to soil disturbance, high soil temperatures and low soil moisture content. Assessment of differential moisture characteristics or $C_{\Theta}(\Psi)$ curve is indicative of changes in structural properties over time. The data from long-term experiments have shown decrease in the macropores and shift to the right of the $C_{\Theta}(\Psi)$ curve due to progressive deterioration in soil structure of an Alfisol in western Nigeria (Lal 1986, 1993).

Inceptisols and Entisols

Psamments are an important group of Entisols in the tropics. These soils occupy about 370 million ha in tropical Africa (Van Wambeke 1992) and about 70 million ha in Brazil (Bowen and Lobato 1988). Psamments are predominantly coarse-textured and are rarely finer than loamy fine sand up to about 1 m depth. Consequently they have a single-grained structure, a relatively high infiltration rate and an extremely low available water holding capacity. In addition to frequent and severe drought stress, these soils have low CEC and are extremely low in inherent soil fertility. Successful plantation growth on Psamments requires soil moisture conservation and judicious use of organic amendments and chemical fertilizers to enhance soil fertility.

Aridisols

These soils have a low organic matter content and a relatively high soluble salt content, and are usually comprised of fine sand and silt fractions. In general, Aridisols have coarse to medium texture with a high proportion of skeletal material comprising gravels, hardened plinthite and remnants of desert pavement. Many are gypsiferous and calcareous, and sand dunes may be a common feature. Consequently, Aridisols are prone to crusting and surface seal formation and to compaction: they are highly compacted even in their natural state. They also exhibit marked hard-setting properties. The surface crust may become hydrophobic due to the formation of an algal layer during the rainy season. The algal crust often decreases the rate of water entry through it to about zero, leading to high runoff, flash floods and severe gully erosion during the rainy season. Wind erosion and sand dune encroachment are problems during the dry season.

Vertisols

High contents of montmorillonitic clay, usually >30% up to 50 cm depth, lead to specific management problems in these soils. These include low infiltration rate, high runoff, susceptibility to erosion by water and poor trafficability when wet. Vertisols are also prone to salinisation, alkalisation and nutrient imbalance. Compaction can also be a problem, especially in the subsoil.

Soil Erodibility and Erosion

Soil erodibility is defined as a soil's susceptibility to erosion, which may be in the order of Aridisols ≥Vertisols > Alfisols > Entisols >Ultisols >Inceptisols >Oxisols >Andisols. All other factors being the same, Alfisols and Entisols are very susceptible to erosion by water and Oxisols and Andisols less susceptible. Soil misuse and exposure to raindrops increase susceptibility to erosion.

The term 'soil erodibility' is also used in predictive models, e.g. USLE (Wischmeier and Smith 1978) and WEPP (Nearing et al. 1994). In the context of these models, erodibility is given a numerical rating to denote relative susceptibility to erosion. In the USLE, erodibility is defined as a ratio of total annual erosion to total annual erosivity (Equation 4):

$$K = A/R \qquad (4)$$

where K is soil erodibility (t R MJ^{-1} mm^{-1}), A is soil erosion (t ha^{-1} yr^{-1}) and R is total annual erosivity (MJ mm $ha^{-1}h^{-1}$). Data from Alfisols in West Africa show that the erodibility factor K of USLE for Alfisols in western Nigeria is low, ranging from 0.0025 under undisturbed vegetation to a maximum of 0.04 t ha h ha^{-1} MJ^{-1} mm^{-1} about three to four yr after change in land use (Lal 1976; Roose 1977). Further, there are marked changes in the erodibility factor with time, with the lowest values occurring soon after the change from native vegetation but reaching the maxima within three to four yr afterwards (Lal 1980). The final or equilibrium value of factor K depends on the subsoil characteristics. Soils underlain with gravelly material obviously have a low K factor because the subsoil material is resistant to erosion. It is well established that erodibility of soils of the humid topics is low (Roose 1977) and it is inversely proportional to cumulative annual erosivity. A detailed discussion of the relationship between the hydrological cycle and soil erosion is given in Chapter 5.

There is a clear distinction between erodibility and erosion. Soils of high erodibility may have less total erosion and vice versa because the magnitude of erosion depends on erosivity, slope and most importantly on soil and crop management. Deforestation and change of land use from native forest and plantation may increase soil erosion and runoff. Lal (1993) showed that sediment concentration was very high during the first year after removal of native forest, and decreased subsequently as the vegetation cover re-established. The data in Table 4.5 from an experiment conducted in western Nigeria indicate that runoff and erosion were in the order of tree-pusher/root rake >shear blade >manual clearing (Lal 1993). In comparison with conversion to arable land use, however, establishment of forest plantation is likely to cause less erosion. Experiments conducted in the Phu Wiang watershed in Thailand showed that runoff and soil losses were the least under forest plantation of *Eucalyptus camaldulensis* (Thongmee and Vannaprasert 1990). Beneficial effects on sediment load of establishing forest plantations were also reported for tropical steep-lands in Sabah, Malaysia (Malmer 1990).

Table 4.5 Effect of deforestation on soil erosion of an Alfisol in western Nigeria (Lal 1993)

Deforestation method	**Year of deforestation**			**One yr after deforestation**			**Two yr after deforestation**		
	1st season	**2nd season**	**Total**	**1st season**	**2nd season**	**Total**	**1st season**	**2nd season**	**Total**
Erosion (t ha^{-1})									
Manual	0.6	0.04	0.64	0.0	0.0	0.0	0.0	0.0	0.0
Shear blade	2.7	1.9	4.6	1.8	0.04	1.84	1.9	0.3	2.2
Tree-pusher/ root rake	21.9	6.7	28.6	0.6	4.2	4.8	0.6	0.01	0.61
Runoff (mm)									
Manual	27.3	3.1	30.4	0.0	0.0	0.0	0.0	0.0	0.0
Shear blade	93.7	61.8	155.5	7.2	45.6	52.8	15.9	5.6	21.4
Tree-pusher/ root rake	170.3	50.9	221.2	14.0	53.0	67.0	20.6	4.8	25.5
Rainfall (mm)	849.7	585.8	1435.5	604.3	845.4	1449.7	642.1	432.4	1074.0

Erosion Control

Erosion control depends on identifying the critical phases of the plantation cycle when soils become vulnerable to erosion and exposure to erosive factors is high. Thus an effective control strategy needs reliable quantitative estimates of: i) soil erosion risks; and ii) erosion effects on soil quality and productivity. Soil erosion risks can be measured by establishing field plots (Mutchler et al. 1994) or using rainfall simulation techniques (Meyer 1994), or by using models, e.g. USLE (Wischmeier and Smith 1978) and RUSLE (Renard et al. 1994). There are also conceptual models including the Erosion/Deposition Process Model (Rose 1994) and WEPP (Nearing et al. 1994). As per the WEPP model, soil erosion comprises inter-rill and rill erosion. Sediment yield from inter-rill areas to rills is estimated by Equation 5:

$$D_i = K_i I^2 \qquad (5)$$

where D_i is rate of inter-rill delivery to rills, K_i is an inter-rill erodibility parameter, and I is average rainfall intensity integrated over the duration of rainfall excess. According to the WEPP, flow detachment in rills is defined as a linear function of flow shear stress (or energy) with a positive intercept on the shear stress axis, which is typically called the critical shear stress of the soil (Nearing et al. 1994; Equation 6):

$$D_c = K_t (\tau - \tau_c) \qquad (6)$$

where D_c is the detachment capacity of the clear water flow, K_t is the soil's rill erodibility, τ is the shear stress of the flow, and τ_c is the soil's critical hydraulic strength. The WEPP model uses a steady-state sediment continuity equation to describe downslope movement of sediment (Equation 7):

$$dG/dx = D_f + D_i \qquad (7)$$

where x (m) represents distance downslope, G (kg s^{-1} m^{-1}) is sediment load, D_i (kg s^{-1} m^{-2}) is lateral sediment flow from inter-rill areas, and D_f (kg s^{-1}) is rill erosion or deposition rate. Net soil detachment in rills is calculated as per Equation 8:

$$D_f = D_c\,[\,1 - G/T_c] \qquad (8)$$

where D_c is detachment capacity by flow and T_c (kg s^{-1} m^{-1}) is the sediment transport capacity in the rill. Net deposition is computed by using Equation 9:

$$D_f = [V_f/q]\,[T_c - G] \qquad (9)$$

where V_f (m s^{-1}) is effective fall velocity for the sediment, and q (m^2 s^{-1}) is flow discharge per unit width (Nearing et al. 1994).

All models have their strengths and weaknesses, and none is universally applicable. Each model should be validated and adapted to site-specific situations. Once risks of soil erosion are known, it is important to assess erosion-induced changes in soil quality and productivity. Methods and guidelines for assessing soil quality are known and standardised (Lal 1994a; Table 4.6). The magnitude of change in soil quality by erosion depends on the severity of erosion and soil profile characteristics. Pierce and Lal (1994) outlined several approaches to assess on-site impact of erosion. In addition to laboratory, greenhouse and field experiments, erosion's impact on soil properties and productivity can be estimated by using statistical or physically-based models. An erosion-productivity minimum data set (EP-MDS) is needed for use of these models. The EP-MDS, however, may need to be developed for principal soils and major plantation species.

The objective of erosion management is to reduce risks to a tolerable level. Risks of accelerated soil erosion can be reduced by decreasing: i) soil's susceptibility to erosion; and ii) kinetic energy of raindrops and overland flow. Several strategies are available to achieve effective erosion control. Important among these is the method of forest conversion for plantation establishment on virgin land, which should be manual or by shear blade to minimise disturbance of the soil surface and to maintain a protective vegetative cover. Establishing an aggressively-growing cover crop immediately after deforestation is a good strategy to minimise erosion, but in commercial plantations skill is required to manage such vegetation so that it does not become an aggressive competitor for critical site resources (water, nutrients and light) and adversely affect tree productivity.

Table 4.6. Suggested methods for assessing soil physical properties (Lal 1994b)

Indicator/Attribute	Method
Texture	International pipet or hydrometer method, correction for gravels
Soil tilth	Tilth index, tilth farming process
Soil structure	(i) WSA > 1 mm and MWD (ii) Bulk density using intact cores (iii) Least limiting water range (iv) Air permeability (v) Crust conductance (vi) Structural indices
Available water capacity	(i) Field capacity *in situ* (ii) Permanent wilting point
Rooting depth	Core-break method
Water transmission	(i) Saturated hydraulic conductivity on intact cores (ii) Infiltration rate (double-ring)
Soil strength	Penetration resistance at known moisture content

The susceptibility of a soil to erosion can be reduced by management of the soil surface and vegetative cover. A practical means of providing a protective ground cover is through growing cover crops between the rows of trees, especially during the early stages of tree growth. In addition to providing ground cover, cover crops are also useful in improving soil physical properties and increasing soil organic matter content. Leguminous cover crops have long been grown in association with plantation crops for these reasons. Cover crops commonly used for this purpose include *Calopogonium muconoides*, *Centrosema pubescens*, *Indigofera spectata*, *Pueraria phaseoloides*, *Stylosanthes guianensis*, *Dolichos hosel*, *Mucuna utilis* and *Galycine javanica*. Kudzu or *Puereria phaseoloides* has been most commonly grown to control soil erosion in oil palm, coconut and other plantations. Cover crops have also been successfully used in erosion control in hoop pine in Queensland, Australia (Dale and Johnson 1991).

The effectiveness of cover crops can be enhanced by runoff management techniques involving engineering structures e.g. terraces, grassed waterways, contour hedges, vegetative barriers etc. Risks of gully erosion on steep slopes can be minimised by drop structures: chutes, gabions and stone riprap.

Synthesis

Soil resources of the tropics are limited, unevenly distributed and prone to degradation. Risks of soil and environmental degradation, however, are more severe with arable land use that involves frequent soil disturbance than with forest land use. The soils and climates of the humid and sub-humid tropics are naturally suited to a forest cover, plantation forestry and root crops. In contrast, the soils and climates of semi-humid and semi-arid tropics are suited to grain crop production. Principal soil-related constraints to sustainable use include water imbalance, nutrient imbalance, low effective rooting depth due to unfavourable soil physical and chemical properties, and high salt concentration in the root zone. These constraints are accentuated by soil degradative processes (e.g. compaction, erosion, leaching and acidification), and vary among soil types and ecoregions. Predominant soils of the humid tropics have low inherent fertility and are deficient in bases (e.g. Ca, Mg, K) and P but contain excessive concentrations of Al, Fe and Mn. These constraints can be alleviated through judicious use of off-farm inputs (e.g. liming and other soil amendments) and choice of appropriate species. Predominant soils of the semi-humid and semi-arid tropics (e.g. Alfisols, Aridisols and Vertisols) are constrained by adverse soil physical conditions. Use of crop residue mulch, cover crops and amendments that enhance soil biodiversity can minimise risks of soil erosion and degradation. Nutritional and soil physical constraints can be overcome by appropriate land use and science-based soil management. The information presented herein supports the following conclusions:

Soils of the tropics are highly diverse and variable. Some soils (e.g. Oxisols, Ultisols and Alfisols) are low in inherent fertility and have severe nutritional constraints. In addition, Alfisols and Inceptisols/Entisols have severe soil physical constraints, e.g. crusting, compaction and accelerated soil erosion. Aridisols and Vertisols are prone to drought and accelerated erosion.

Land misuse and soil or tree mismanagement can cause soil degradation even with plantation forestry and tree crops. However, judicious soil and vegetation management can improve soil properties, minimise soil erosion risks and enhance soil quality and productivity.

Physical properties of soils under natural forest cover are favourable and characterised by a high degree of aggregation, high infiltration rate and low soil bulk density. Deforestation and change in land use for establishing plantation forests can lead to compaction, erosion and depletion of soil organic matter, and thus degradation of soil physical and nutritional properties.

Erodibility of soils of the tropics, as defined in the USLE, may be low for soils of the humid regions and high for those of the sub-humid, semi-arid and arid regions. Soils of the semi-arid tropics are prone to high erosion rates due to adverse slope, poor soil surface management and high rainfall/runoff erosivity. Soil erosion risks are generally high prior to the development of canopy cover.

An effective erosion management strategy involves: i) assessment of soil erosion risks; ii) evaluation of erosion impact on soil quality; and iii) decreasing soil erodibility, and rainfall and runoff erosivity. Growing leguminous cover crops in association with trees is a useful strategy for improving soil properties and controlling erosion.

Very high and rapidly increasing population pressure and harsh climates necessitate a systematic evaluation of properties and processes of soils in the tropics with the objective of defining potential and constraints, identifying appropriate land use, and adopting sustainable methods of soil and water management. Priority tasks are to identify and define critical limits to key soil properties in relation to productivity for different plantation systems, assess relationship between soil properties, climate and soil degradative processes, evaluate the effects of plantation management systems and other land uses on long-term changes in soil quality, and establish soil quality indices based on an understanding of the relationship between soil properties and productivity.

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5

Hydrology of Forest Plantations in the Tropics

L.A. (Sampurno) Bruijnzeel

Abstract

The stage of development of plantations, and their management, greatly influence their hydrological characteristics. The largest changes in catchment water yield, runoff response and sediment yield associated with plantations usually occur when natural forest is converted to plantation. Effects on peak streamflow rates and sediment loads normally stabilise within two yr of establishment at levels slightly above the original values. Comparatively little is known of the water use of even the most commonly-planted species. As a result, no sound predictions of the eventual effects of plantations on the magnitude of annual and seasonal water yield are possible at this stage. However, there is evidence that the planting of fast-growing trees on grassland will diminish streamflow after canopy closure, particularly during the dry season. The hydrological effects of forest management practices and the usefulness of catchment hydrological models in predicting such effects are discussed. It is concluded that, although relatively little is known at present of the hydrology of tropical plantations in relation to interactions between climate, soils and tree species, the methodology to fill the major gaps in knowledge is well established.

AN UNDERSTANDING of the hydrology of plantations is important for several reasons—plantations are often situated in catchments which provide water for other land uses or urban purposes, and thus the quality and quantity of the water yield may be critical; the common combination of hilly topography and moderate or high rainfall at plantation sites is potentially conducive to erosion and/or operational difficulties, and not least the water relations of the plantation site have a profound influence on the choice of species (Chapter 2), nutrition and plantation growth.

Whilst in many parts of the humid tropics indiscriminate clearing of natural forest has led to serious degradation of soils and streamflow regimes, reforestation will not always lead to the restoration of the original hydrological conditions (Hamilton and King 1983). Improved flows have been claimed following reforestation (e.g. Hardjono 1980) but in other cases the planting of fast-growing trees on grass- and scrublands has considerably decreased dry-season water yield (Mathur and Sajwan 1978; Smith and Scott 1992; Waterloo 1994).

Concern has also been expressed about the potential loss of soil fertility by repeated harvesting of plantations (Hase and Fölster 1983; Russell 1983; Bruijnzeel and Wiersum 1985). The close linkage between the forest hydrological cycle and overall nutrient inputs and outputs is well-established and can be best evaluated by choosing a (watertight) catchment area as the fundamental unit (Bormann and Likens 1967). In addition, small catchments may also provide a suitable framework for the study of solute losses associated with forest disturbance and clearing (Likens et al. 1977).

This chapter aims to: i) provide a hydrological basis for the quantification of the nutrient budget at various stages of the plantation life cycle (as discussed further in Chapter 10); ii) reconcile conflicting evidence of the influence of plantations on water yield; and iii) examine hydrological impacts of various forest management options. The issues arising are examined and discussed from the viewpoint of general hydrological principles.

The account starts with a brief discussion of the forest hydrological cycle, followed by an analysis of the respective hydrological impacts (changes in water yield, infiltration capacity, peak flow and sediment yield) of different methods of forest clearing and site preparation. Next, the changes in hydrological characteristics (rainfall interception, stand water use) associated with the development and maturation of a plantation are discussed. This discussion is generally illustrated with data from the tropics, but where such information is lacking pertinent data from warm-temperate regions are used. Subsequently, the hydrological impacts of various forest management activities, and measures to minimise any adverse consequences during plantation establishment and harvesting, are considered. Finally, after identifying the most important gaps in our knowledge, a case is made for the establishment of a network of sites at which research can be concentrated on the most important species used in tropical plantations.

The Forest Hydrological Cycle

The principal features of the forest hydrological cycle are illustrated in Figure 5.1. Rain is the main precipitation input to the forests of the humid tropics. A small part of the rain reaches the forest floor as direct throughfall and stemflow. A substantial portion of that intercepted by the forest canopy is evaporated back into the atmosphere during and immediately after the storm; the remainder reaches the soil surface as crown drip. Because direct throughfall and crown drip cannot be determined separately in the field, the two are usually taken together and referred to as throughfall. If the intensity of the total throughfall and stemflow reaching the forest floor exceeds the infiltration capacity of the soil, the unabsorbed excess runs off as 'Hortonian overland flow' (HOF). Due to the generally very high absorbing capacity of the organic-rich topsoil in most native tropical forests, the bulk of the throughfall

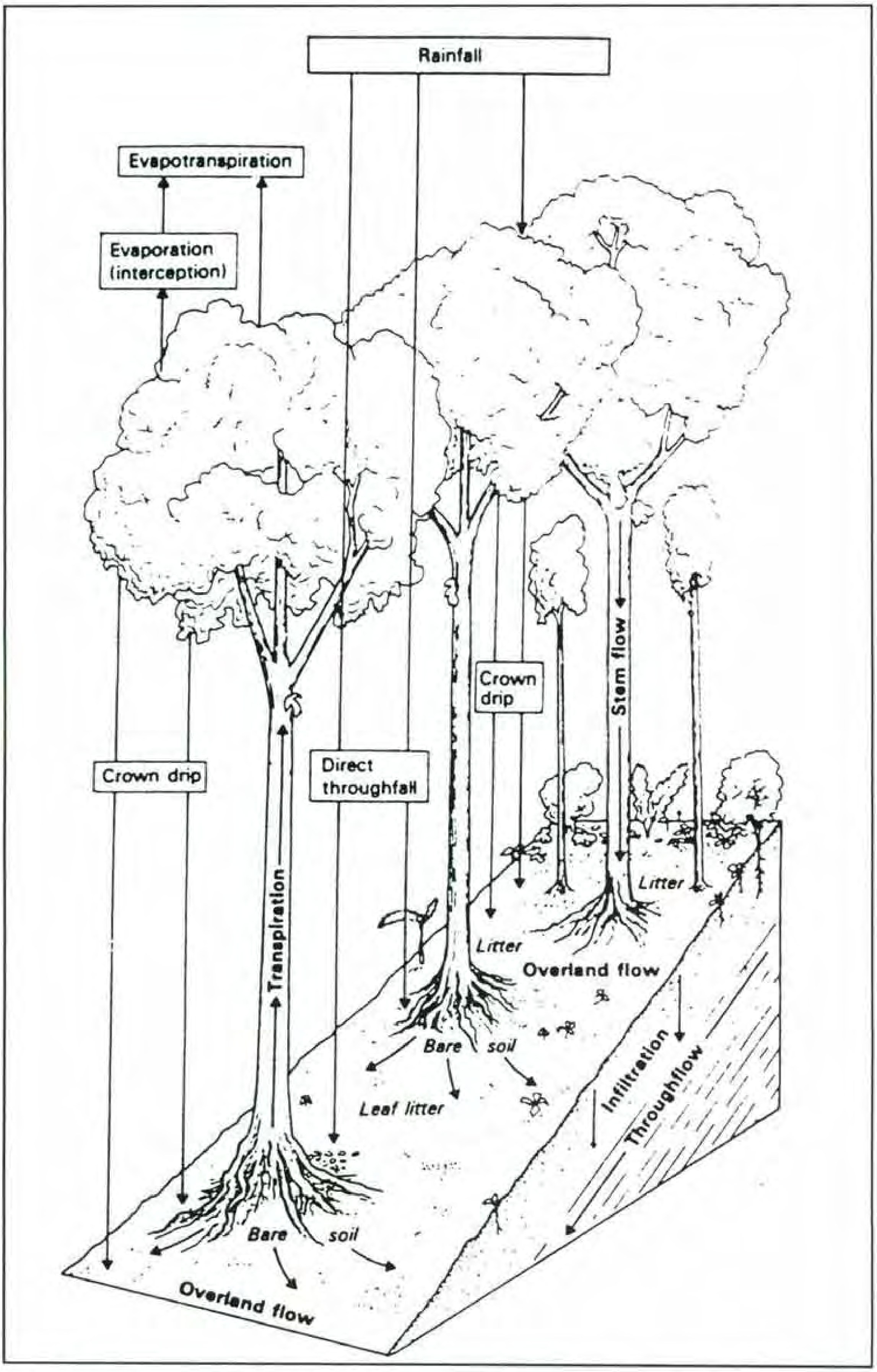

Figure 5.1 The hillslope forest hydrological cycle (modified from Douglas 1977)

and stemflow will generally infiltrate the soil and thus this type of flow occurs relatively infrequently. Much of the infiltrated water is taken up by the vegetation and returns to the atmosphere via the process of transpiration (Et). The term evapotranspiration (ET) is used to denote the sum of transpiration (evaporation from a dry canopy) and interception loss (Ei, evaporation from the exposed surfaces of a wet canopy). Evaporation from the litter and soil surface (Es) in (humid tropical) forest is usually negligible. It is important to make the distinction between Et and Ei because the former is governed largely by stomatal control and the latter mostly by the aerodynamic properties of the vegetation (Jarvis and Stewart 1979; Chapter 6).

The remaining soil moisture drains into the stream network by 'throughflow', the result of downward-moving water meeting an impermeable layer of subsoil or bedrock and being deflected laterally (Fig. 5.1). Such water drains slowly and steadily, thus accounting for the 'baseflow' of streams (Ward and Robinson 1990). In seasonal climates, baseflow reaches a minimum in the dry season and this is referred to as 'dry-season flow'.

During rainfall, infiltrated water may take one of several routes to the stream channel, depending on soil hydraulic conductivities, slope morphology and the spatial distribution of soil moisture (Dunne 1978). 'Saturation overland flow' (SOF) is caused by rain falling onto an already saturated soil. This typically occurs in hillside hollows or concave footslopes near the stream where subsurface flow tends to converge and so maintains near-saturated conditions. Additionally, SOF can be observed during and after intense rainfall where an impeding layer is found close to the surface (Bonell and Gilmour 1978). 'Subsurface stormflow' (SSSF) often represents a mixture of 'old' (i.e. already present before the start of the rain) and 'new' water travelling rapidly through 'macropores' and 'pipes' (Bonell and Balek 1993). As a result of contributions by SOF, SSSF, and in extreme cases HOF, streamflow usually increases rapidly during rainfall. This increase above baseflow levels is often called 'stormflow' or 'quickflow'. The highest discharge is commonly referred to as 'peak flow', and this may be reached during the rainfall event itself or as late as a few days afterwards, depending on catchment characteristics and wetness, as well as on the duration, intensity and quantity of the rainfall (Fig.5.2; Dunne 1978). The total volume of water produced as streamflow from a catchment over a given period of time (usually a month, season or year) is called 'water yield'.

The interlocked character of the chief components of the catchment hydrological cycle is illustrated by the water budget equation (Ward and Robinson 1990):

$$P = ET + Q + \Delta S + \Delta G \qquad (1)$$

where

P = precipitation

ET = evapotranspiration

Q = streamflow

ΔS = change in soil water storage

ΔG = change in groundwater storage

with all values expressed in mm water per unit of time (day, week, month or year).

Furthermore:

$$ET = Ei + Et + Es \qquad (2)$$

and

$$Ei = P - (Tf + Sf) \qquad (3)$$

where

Tf = throughfall

Sf = stemflow

Detailed quantitative descriptions of the hydrological cycle of tropical rainforest have been given by Bruijnzeel (1990) and Bonell and Balek (1993).

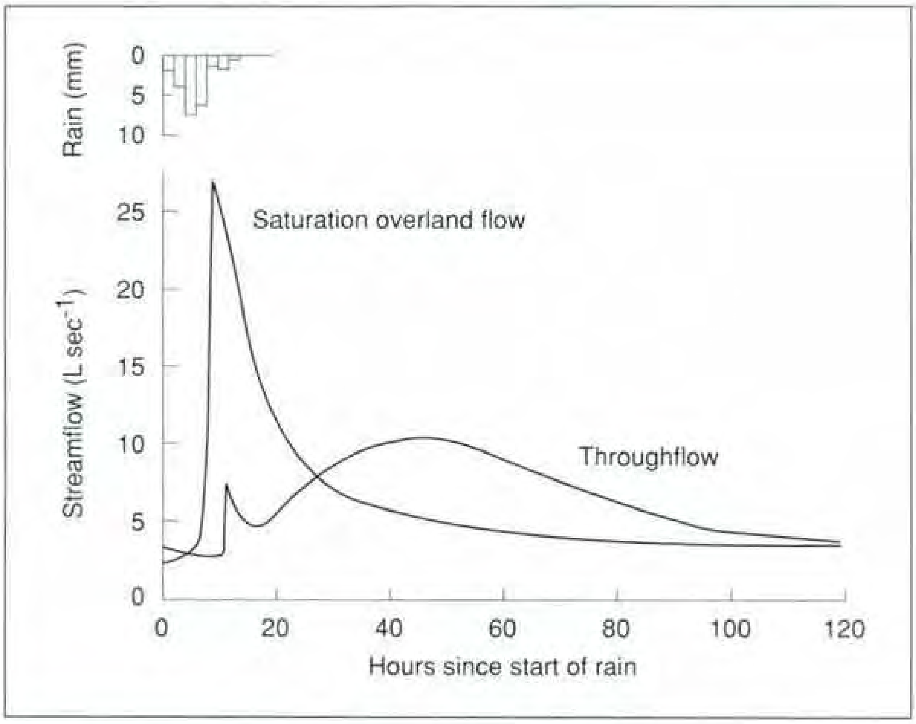

Figure 5.2 Catchment response to rainfall (modified from Calver et al. 1972)

Hydrology of Forest Plantations

The establishment of a plantation entails a number of practices which affect the hydrological properties of the soil, catchment hydrological response and tree growth. Generally, soil disturbance will be greater when plantations are established on natural forest land than when reforesting grassland. In the former case heavy mechanised equipment is often used to harvest large tree trunks and for site preparation, including the 'windrowing' of logging debris, whereas for reforesting grassland, burning and less intensive site preparation will suffice.

In view of the similarities between natural forest and mature plantations, it could be argued that the largest changes in hydrology associated with the conversion from one to the other can be expected during the first 1–3 yr after forest clearing and replanting, i.e. in the 'establishment' phase. The first 6–12 months of this are particularly critical because most of the soil surface will be exposed. Levels of peak discharge and erosion tend to return to predisturbance values within the next two yr due to the establishment of a vigorous understorey. However, the amount of water percolating through the soil (and hence amount of nutrients leached) will remain well above the original level during this period (cf. Malmer and Grip 1994). Subsequently, during 'stand development and maturation', there will be a gradual return to preconversion conditions. Hydrological changes during the establishment and maturation phases will therefore be discussed separately. When developing a plantation on grassland, the initial changes in hydrology will be smaller than those seen when starting with an already-forested site, while the maximum contrast will occur upon the stand reaching maturity (Smith and Scott 1992).

The establishment phase

Effect of clearing on soil physical properties

When heavy machinery enters undisturbed forest the protective litter layer will be disrupted. Topsoil bulk density will increase through compaction, particularly in the case of wet and clayey soils, and the water-holding and transmitting capacity of the soil will be reduced (see Chapter 4 for a general description).

Couper et al. (1981) compared several methods of forest clearing on an Alfisol in Nigeria in terms of man-hours and energy expenditure. Lal (1981) reported on the associated surface runoff and erosion rates for (no-tillage) agriculture during the first year after clearing. Whilst manual clearing was the slowest and most 'expensive', soil erosion was as low as 0.4 t ha^{-1} yr^{-1}, compared to c. 4 t ha^{-1} yr^{-1} after clearing with a crawler tractor with a shear blade, and 15 t ha^{-1} yr^{-1} after a crawler tractor with a tree pusher/root rake. Values of surface runoff were 1%, 6.5% and 12% of incident rainfall, respectively. More details are given in Tables 4.4 and 4.5 of Chapter 4.

Similarly, Dias and Nortcliff (1985b) reported negligible change in physical topsoil properties after traditional slash-and-burn clearance of a forest on a clayey Oxisol in Amazonia. However, considerable deterioration followed clearing by bulldozer, both because of compaction and because the removal of litter and topsoil exposed subsoil with less favourable properties (cf. Gillman et al. 1985; Malmer and Grip 1990). On clayey Oxisols and Ultisols, Dias and Nortcliff (1985a) and Kamaruzaman Jusoff (1991), respectively, reported a close relationship between the number of tractor passes and the resulting degree of compaction. In both cases, soil deterioration increased with soil wetness. Wheeled machinery had considerably greater impact than tracked vehicles (Fig. 5.3), particularly after wheel slippage. Effects usually extend to 15–20 cm depth and, in the case of former log haulage tracks, show very little improvement even after many years of nonusage (Hendrison 1990; Van der Plas and Bruijnzeel 1993).

Because of their skeletal structure, sandy soils show a different response to disturbance. Mechanised clearing of forest on podzols in East Malaysia did not result in a major increase in topsoil bulk density although final infiltration rates were reduced considerably (from 48.7 down to 1.3 mm hr^{-1}; Malmer and Grip 1990). However, with the exception of valley bottoms, saturation will rarely occur in sandy soils. It is important, therefore, to examine the effects of soil disturbance over a range of moisture conditions, as represented by soil water retention and unsaturated hydraulic conductivity curves. Jetten (1994) compared such curves for two types of sandy soils in Guyana before and after disturbance by wheeled skidders. White sand soils were most affected by repeated passage of machinery. Their retention curves became more gradual, i.e. suction values for a given moisture content increased as a result of a shift in pore distribution towards finer pores. Unsaturated hydraulic conductivities decreased accordingly, particularly at the wetter end of the suction range. The explanation may lie in the compaction of the originally loosely packed sand but possibly also in the mixing of fine organic matter with soil mineral particles. The effect was less pronounced for loamier brown sand soils, but here the changes occurred over the entire moisture range (Jetten 1994). Although manual methods of forest clearing cause less damage to the soil surface than does mechanical equipment, there will often be no choice but to resort to mechanical means.

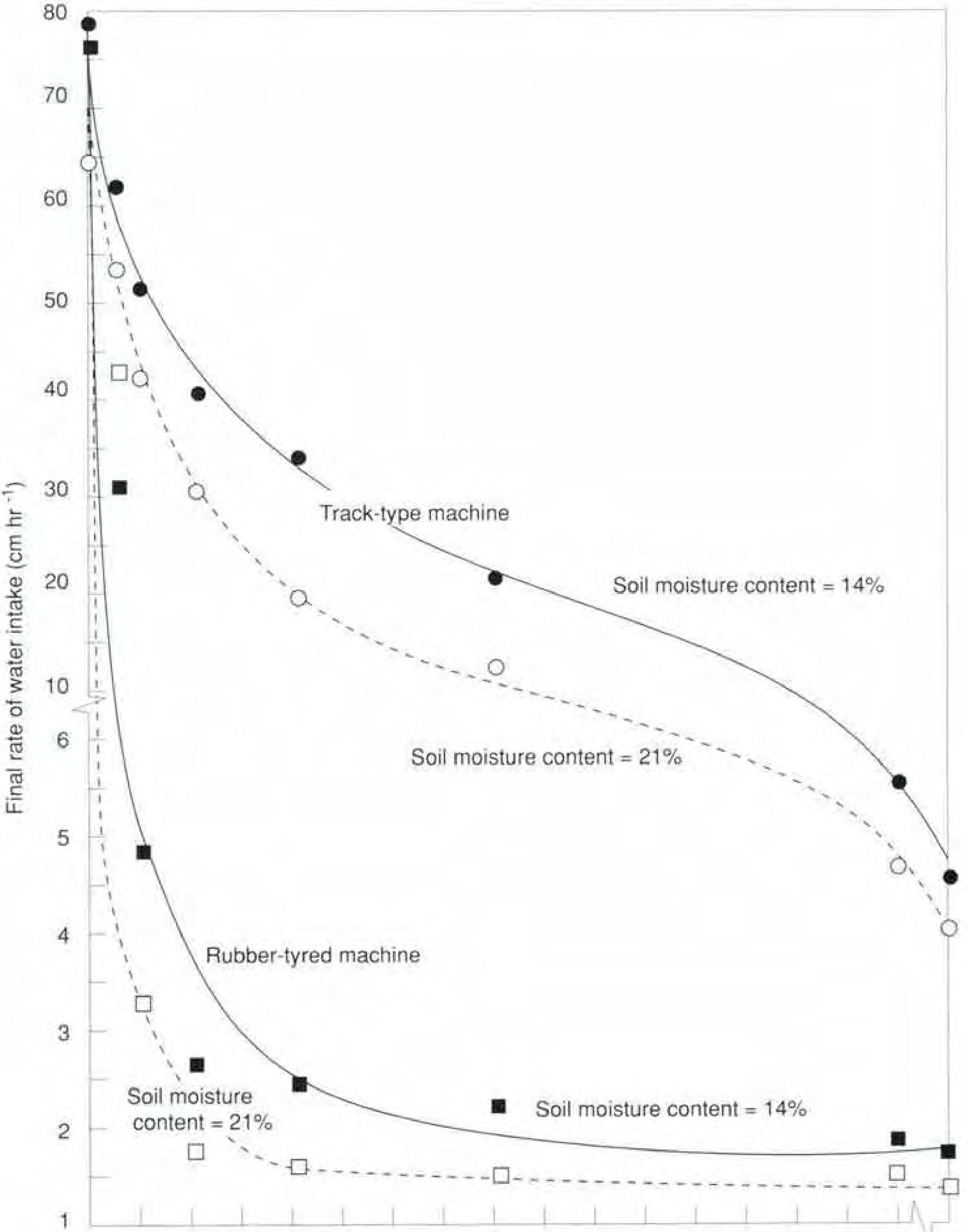

Figure 5.3 The impact of wheeled and tracked vehicles on saturated topsoil hydraulic conductivity as a function of the number of vehicle passes and soil wetness for an Ultisol in Peninsular Malaysia (adapted from Kamaruzaman Jusoff 1991)

Effect of clearing on catchment water yield

The removal of vegetative cover to establish a new plantation will temporarily reduce ET and hence increase catchment water yield. Bosch and Hewlett (1982) demonstrated this for about 100 cases from all over the world, including a few examples from the tropics. The most recent data set confirms that the initial increase in water yield is proportional to the amount of biomass removed (Bruijnzeel 1996a).

The reported increases in flow during the first three yr range from 125 to 820 mm yr^{-1}, with an average value of about 600 mm yr^{-1} (Bruijnzeel 1990, 1996). Whilst there is a weak tendency for larger increases to occur in high rainfall areas, the scatter in the data is large (Fig. 5.4). There are strong indications that the severity of soil disturbance is as important as post-clearing rainfall (Fig. 5.4). Malmer (1992) compared the changes in water yield in the first 2.9 yr of an *Acacia mangium* plantation after clearcutting rainforest in Sabah, East Malaysia, that had been selectively logged about six yr before the experiment. The different treatments were: 1) manual felling and extraction of timber followed by manual planting in rows between logging debris that had been left to rot; and 2) manual felling with timber extraction by crawler tractors, followed by burning of the slash (no windrowing) and planting. Whilst the increase in runoff was somewhat lower during drier years for both treatments (Fig. 5.4), overall increases were far smaller following manual extraction without burning than for mechanical harvesting plus burning (viz. 445 vs. 1190 mm; Malmer 1992).

Within the same experiment the secondary vegetation of an adjacent catchment that had been struck by an intense forest fire about five yr previously was burned again experimentally before planting it to *Acacia mangium*. The increase in streamflow over the same 2.9 yr was 1010 mm (Malmer 1992). Although these figures illustrate the potential for increased nutrient losses via leaching after clearing under wet tropical conditions, particularly where this is done in conjunction with burning (cf. Bruijnzeel 1996b; Chapter 10), it is impossible to separate the effects of mechanised clearing and burning in this particular experiment (see Bruijnzeel (1995) for details).

Effects of clearing on stormflow volume and peak discharge

The magnitude of the various flow components contributing to stormflow will vary between catchments as a result of differences in topography, soils (notably hydraulic conductivity) and rainfall characteristics (Dunne 1978; Pearce et al. 1982). The effect of the soil factor is illustrated by the results obtained for ten small (<1.5 ha) rainforested catchments in the perhumid (annual rainfall ca. 3500 mm with no clear dry season) lowlands of French Guyana, all close to each other (Fig. 5.5). Storm runoff ranged between 7.3% of rainfall (catchment h) and 34.4% (catchment e),

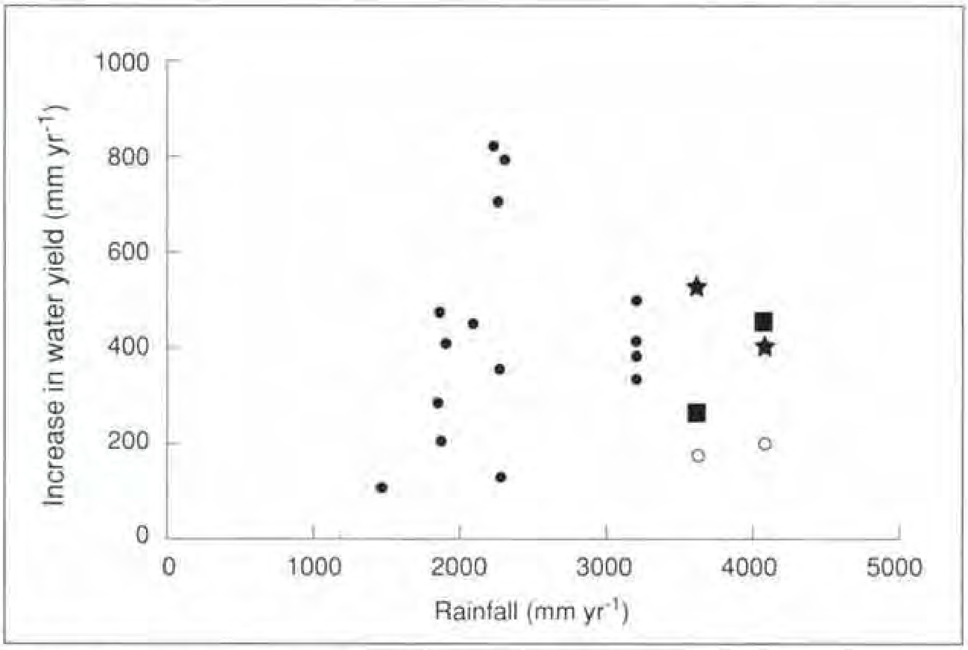

Figure 5.4 Increases in water yield after clearing tropical forest vs. corresponding amounts of rainfall (modified from Bruijnzeel 1995). The results for three adjacent catchments in East Malaysia (W1, W4 and W5), in the two yr following clearing in different ways are identified: Catchment W1, nonmechanised clearing followed by burning of slash = ★; catchment W4, manual extraction of logs, no burning = ○; catchment W5, mechanised harvesting, followed by burning of slash = ■ (Malmer (1992). Observations from other studies = ●

depending on soil type. The proximity of the groundwater table to the surface in the valley bottom at the height of the rainy season governed catchment response, and the larger the proportion of well-drained soils the smaller the runoff response (Fritsch 1992).

Normally, streamflow peaks that are produced by overland flow tend to be more pronounced than those generated by slower-travelling subsurface flow (Fig. 5.2). A shift from a slow throughflow-dominated stormflow pattern in forest to one that is governed by HOF after clearing may produce substantial increases in peak flows. However, in catchments where overland flow is already rampant under natural conditions, the hydrological response to rainfall (but not that of soil erosion) is hardly changed after forest removal (Gilmour 1977). Such a situation may occur where an impeding layer at shallow depth leads to widespread hillslope SOF (Bonell and Gilmour 1978) or pipeflow (Elsenbeer and Cassel 1990). All this points to the need for proper pedo-hydrological (in addition to standard soil) survey for assessing the hydrological impact of forest management practices.

Carefully planned and conducted conversion operations will be able to keep the area of compacted soil, and hence increases in the frequency and magnitude of HOF, to a minimum, particularly in the absence of burning (Hsia 1987; Malmer 1993). However, even with minimum soil disturbance, stormflow volumes and peak flow rates may increase after forest removal. This is because the associated reduction in ET will lead to wetter soils which will be less capable of accommodating additional rainfall. In addition, this extra moisture will maintain a wider saturated strip along the stream which, in turn, will yield a larger volume of (SOF-dominated) storm runoff. Wherever topography permits expansion of this riparian 'source area' sufficiently, the effect will be noticeable, particularly after dry periods when under forested conditions the source area will have reached a minimum (Hewlett and Doss 1984; Fritsch 1992). Estimates of the increases in stormflow after clear-cutting with minimum soil disturbance may be derived from an experiment in a high rainfall area in New Zealand where runoff was dominated by subsurface flow (Pearce et al. 1980). Relative increases (as compared to a forested control basin) in stormflow volume were 100%–300% for small rainfall events (say <10 mm); c. 50% for intermediate storms (25–50 mm); and 10%–25% for large (>75 mm) storms. The effect is thus seen to diminish as rainfall increases. In a similar experiment in a steep catchment in Taiwan, no significant change in stormflow volume was observed but the median value of peak discharge rate increased by almost 50% as a result of the increased wetness of the hillslopes (Hsia 1987).

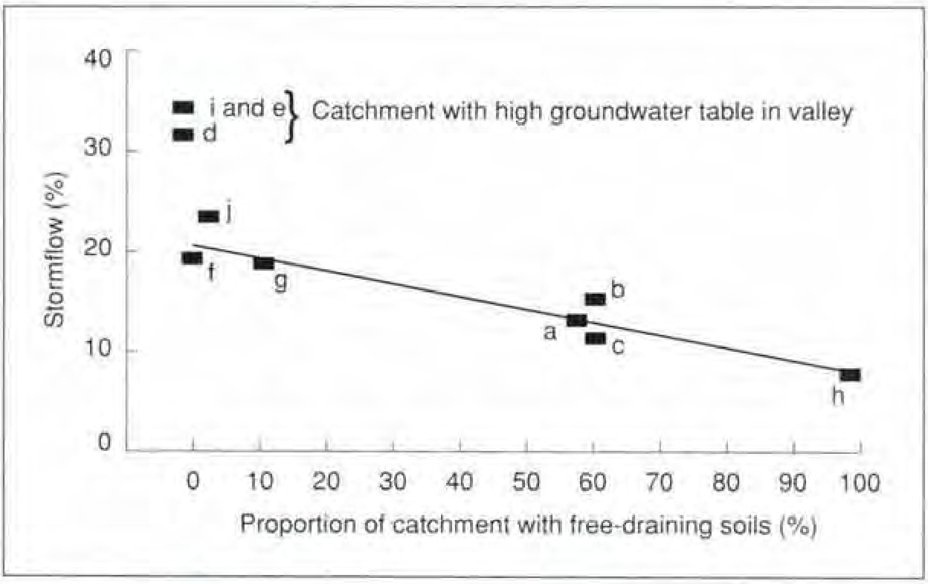

Figure 5.5 Runoff response (stormflow as a percentage of annual rainfall) of small forested catchments in French Guyana as a function of the proportion of catchment area underlain by free-draining soils (modified from Fritsch 1993)

When soils are more extensively disturbed by heavy machinery and/or fire for plantation establishment, the resulting changes in catchment response can be expected to be more pronounced. Yet, few unambiguous results have been obtained in this respect, possibly because the complexity of the runoff generation process often defies the simplicity of our analytical techniques (Hewlett 1982). For example, in the experiment by Malmer (1992) in East Malaysia, both stormflow volumes and peak discharges increased significantly during the first two yr after burning a catchment that had been struck by a natural forest fire several years previously. On the other hand, the only significant change that was observed after mechanically clearing the vegetation and burning the slash in a nearby catchment, was a reduction in stormflow volume during the first year, even though the soil had become severely disturbed over 24% of the area (Malmer and Grip 1990). During the second year after clearing, stormflow volumes and peak discharges increased again but not significantly. Malmer (1992) interpreted these findings in terms of contrasts in surface detention characteristics between the two catchments. For instance, water was initially seen to be standing in the ruts of former tractor tracks which then started to erode during the second year. Similarly, Swindel et al. (1983a) reported a sixfold increase in peak discharges immediately after mechanically clearing and burning a *Pinus elliottii* flatwood forest in north Florida. This was followed by a gradual decline over the next 18 months. Yet, no changes were observed in the correspondingly increased stormflow volumes throughout the two-and-a-half yr post-clearing observation period (Swindel et al. 1983b). Normally, such increases tend to diminish within a few years as the new vegetation becomes established, unless they are associated with structural changes in the runoff generation process, for example due to the construction of roads or the creation of active gullies. These findings point to the value of process studies in support of the traditional 'black box' paired watershed approach.

A major experimental investigation into the effects of tropical forest conversion on stormflow volumes, peak discharges and erosion has been conducted in French Guyana (Fritsch 1992, 1993). Ten small forested catchments with different admixtures of freely- and/or poorly-drained soils were gauged for two yr (cf. Fig. 5.5) before being subjected to a variety of treatments, including forest regeneration after logging or slash-and-burn agriculture, and conversions to grassland or plantations of *Pinus caribaea* and *Eucalyptus grandifolia*, whilst two catchments remained undisturbed as controls (Fritsch 1992, 1993).

Although the different hydrological behaviour of the respective catchments under undisturbed conditions (Fig. 5.5) precludes a direct comparison of the effect of each treatment, several interesting comparisons are possible (Fig. 5.6). For example, the similarity in predisturbance runoff response of catchments a, b and c (Fig. 5.5) enables an evaluation of the effects of logging (catchment a), mechanical clearing (catchment b) and traditional clearing (catchment c). Logging followed by regeneration produced only minor increases in stormflow (2%–4%), with a maximum increase (26%) during the (wet) third year and no detectable increase in the fifth year (Fig. 5.6a). Peak discharge increased (by 13%) during the first year only. In contrast, where logging was followed by mechanical clearing and burning, stormflow volume increased by about 150% during the first year (Fig. 5.6b). With the establishment of the regrowth in subsequent years, this value dropped rapidly to 40% in the second year and to 16% in the fourth year. Peak discharge showed a marked increase only during the first year (42%) but not during subsequent years (Fritsch 1992). Changes in both stormflow volume and peak discharge associated with slash-and-burn were 26–30% during the two yr of cultivation (Fig. 5.6c). Although these values are much smaller than the ones observed immediately after mechanical clearing, there is nevertheless a clear effect.

The two catchments converted to forest plantations (d and e) showed the greatest runoff response in the undisturbed state (Fig. 5.5). The relative increases in stormflow volume or peak discharge after clearing (Figs 5.6d and 5.6e) may therefore look smaller than those in some other cases. The absolute increases during the first rainy season after clearing on these two catchments were however quite high (viz. 560–620 mm compared to 245 mm for catchment b where natural regrowth was allowed; Fritsch 1993). The increase in hydrological response decreased with time (Figs 5.6d and 5.6e), although not as fast as in the case of natural regrowth after clearing (Fig. 5.6b), as the plantations had to be weeded several times during these early years. The corresponding increases in peak discharges were 55–65% during the first two yr but declined rapidly afterwards (Fritsch 1992). By the sixth year, increases in stormflow had become negligible (Figs 5.6d and 5.6e).

It is of interest to also examine the effects of conversion from forest to grazing land on catchment response because this could indicate what may be expected after the reforestation of grassland. In the undisturbed state, the catchment that was to be converted to *Digitaria* grassland (catchment f) showed a runoff response of intermediate magnitude (Fig. 5.5). Following conversion, increases in stormflow volume remained substantial throughout the first four yr (generally >50%), with a somewhat lower value (27%) in the fifth year (Fig. 5.6f). Levels of peak discharges were consistently about 75% higher than expected under forested conditions (Fritsch 1992). These figures illustrate the considerable reductions in runoff that may follow reforestation of tropical grasslands.

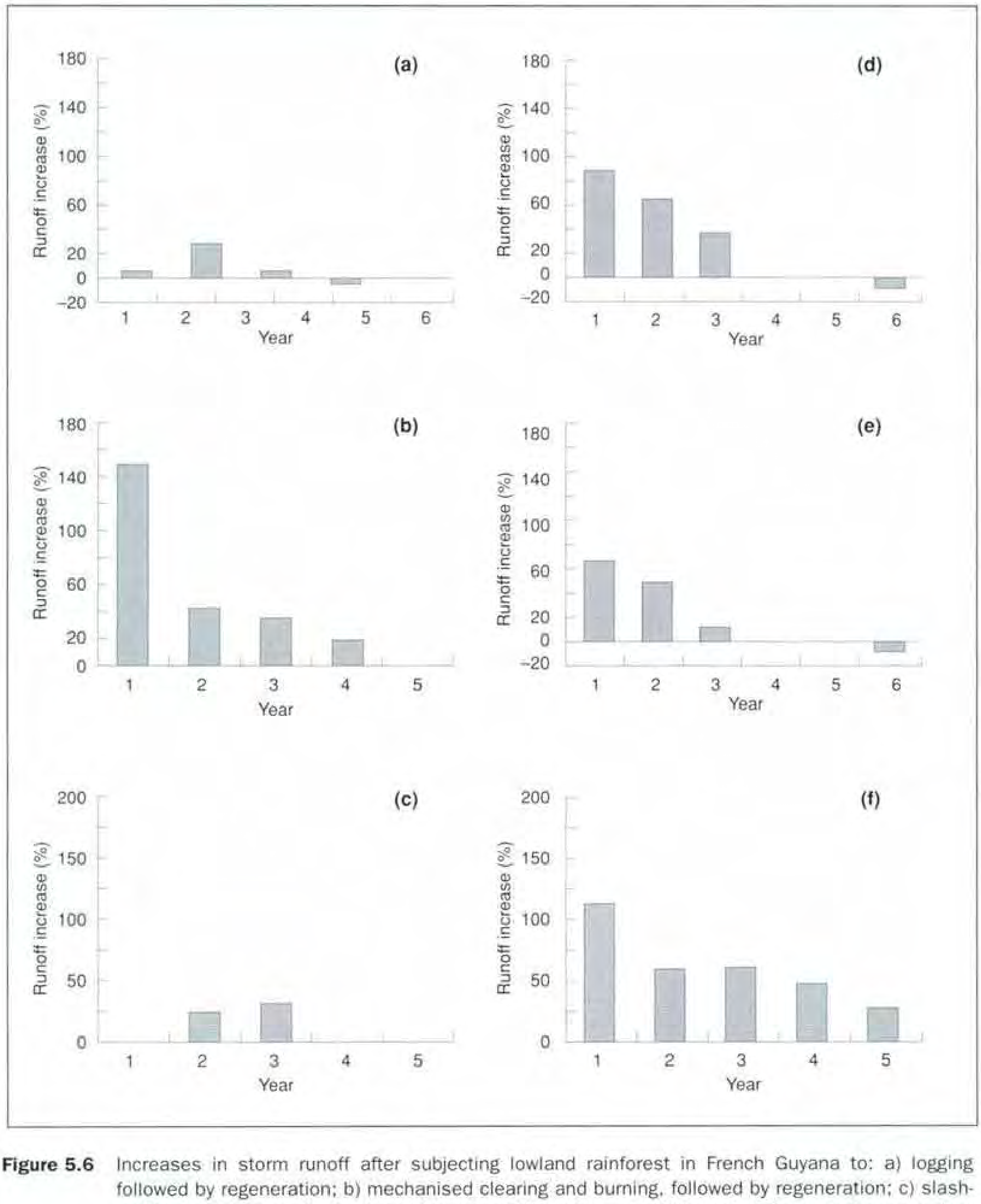

Figure 5.6 Increases in storm runoff after subjecting lowland rainforest in French Guyana to: a) logging followed by regeneration; b) mechanised clearing and burning, followed by regeneration; c) slash-and-burn cultivation; d) clearing and burning, followed by establishment of *Pinus caribaea*; e) idem for *Eucalyptus grandifolia*; f) idem for *Digitaria* grassland (modified from Fritsch 1993)

Effect of clearing on basin sediment yield

There are several different forms of erosion. Splash erosion is the process by which soil particles are detached by the impact of rain drops on the soil surface. The eroded particles, which may have been moved only a few centimetres, are then susceptible to further transport downslope by overland flow (sheet erosion). Both splash and sheet erosion are of little importance in most undisturbed forests, but they may well produce substantial amounts of sediment after the soil is bared. Once this stage is reached, topographic irregularities often lead to the concentration of overland flow in 'rills'. If the process continues long enough, these rills may deepen and widen into gullies. 'Mass wasting' is another mechanism of sediment supply to streams, especially common in steep areas where rainfall is high. Landslips and riverbank erosion fall into this category, and are often a natural hazard. The magnitude of sediment production under forested conditions depends on the relative importance of the respective contributing mechanisms (Pearce 1986). Sediment yield from rainforested catchments may be as low as 0.25 t ha^{-1} yr^{-1} in stable areas underlain by deep permeable soils that are neither subject to significant sheet erosion nor mass wasting (Douglas 1967). Yet, in tectonically active tropical steepland areas prone to hillslope failure, such as are frequently found along the Pacific rim, this figure may well approach 40 t ha^{-1} yr^{-1} during wet years (Dickinson et al. 1990) or more in specific cases (e.g. over 65 t ha^{-1} yr^{-1} for unstable marly soils; Van Dijk and Ehrencron 1949; Bell 1973). Any effects of forest clearing will be most evident where natural rates of sediment production are low.

It is important to recognise that not all eroded material is delivered directly into the stream network. Particles are often trapped temporarily (or permanently) in depressions in the terrain or deposited on footslopes or alluvial plains. This is especially true for splash and sheet erosion, and explains why it is not possible to predict catchment sediment yields from observations of erosion made on small hillside runoff plots alone. On the other hand, gully erosion, large landslides and riverbank erosion deliver sediment directly into the stream. The arrival of sediment at the stream network or its immediate surroundings, however, does not mean it will appear downstream immediately. An exceptional peak flow may be necessary to wash previously-deposited sediment into its final resting place. Thus the effects of soil disturbance tend to be first manifest on hillslopes in the form of increased sheet erosion and only later as increased catchment sediment yield (Walling 1983; Bons 1990).

Whilst it is difficult to quote 'typical' values for increases in hillslope erosion and catchment sediment yield accompanying forest conversion in the humid tropics, an idea can be gained from the results obtained by the studies by Malmer (1990) in East Malaysia and by Fritsch and Sarailh (1986) in French Guyana. Both experiments took place in high rainfall areas (>3500 mm yr^{-1}) with low background sediment yields before clearing.

The changes in yield of suspended sediment from the catchment associated with the conversion of rainforest to a plantation of *Acacia mangium* in East Malaysia can be summarised as follows. Pre-disturbance values were very low at 0.05 and 0.2 t ha^{-1} yr^{-1} for two catchments, W4 and W5, respectively. Catchment W4 was then cleared manually without burning of slash whilst catchment W5 was cleared mechanically and burned. Increases in sediment yield during the period of clearing plus the next five months necessary to reestablish the understorey in catchment W5 were six- and tenfold for catchments W4 and W5, respectively. Surprisingly, in view of the different treatments, sediment production over the next ten months was equal in both catchments. Compared to the preceding eight-month period, this represented a threefold increase in the case of catchment W4 but a 50% reduction for catchment W5. Malmer (1990) interpreted the unexpected finding for catchment W4 in terms of suppressed understorey vegetation due to the presence of large amounts of slash. Also, the slash had been arranged in rows running down the slope and this may have influenced the occurrence of surface runoff as well. However, the overall effects were relatively shortlived. Catchment sediment yields were virtually back to normal within 20 months after clearing. Total sediment exports from the catchments during the first three yr after clearing were 2.3 and 4.1 t ha^{-1} for catchments W4 and W5, respectively. By contrast, surface erosion on former tractor tracks in catchment W5 exceeded 500 t ha^{-1} during the same period (Malmer 1993), suggesting that considerable volumes of sediment went into storage.

Sediment outputs from the catchments in French Guyana studied by Fritsch and Sarrailh (1986) ranged between 0.05 and 0.75 t ha^{-1} yr^{-1} before disturbance, depending on stormflow regime and soil type (cf. Fig. 5.5). Despite the very similar preclearing runoff behaviour of the two catchments converted to plantations of pine and eucalypt (catchments d and e; Fig. 5.5), increases in sediment yield during the first year after clearing differed markedly (50- and 16-fold increases to 17 and 6 t ha^{-1} yr^{-1}, respectively). This unexpected contrast can be explained by the fact that the valley bottom of catchment e had become surrounded by walls of earth and slash acting as a filter for sediment coming from upslope (Fritsch and Sarrailh 1986). An independent survey estimated average hillslope erosion at about 1200 t ha^{-1} (Fritsch 1983). Such contrasts between on-site erosion and off-site sediment yield underscore the point made earlier about possible discrepancies between the two (cf. Bons 1990). No information has been published on sediment yields for these catchments during subsequent years but observations for a nearby catchment converted to grassland suggested a rapid decline in sediment yield during the second and third year after clearing (to a stable value of about 0.5 t ha^{-1} yr^{-1}, or three times the value expected under forested conditions), compared to an initial 34-fold increase to 12 t ha^{-1} yr^{-1} during the first year (Fritsch and Sarrailh 1986).

Much more modest increases in sediment yield (i.e. less than double the values observed under forest) may be obtained when using skyline log extraction techniques, as has been demonstrated by Pearce et al. (1980) and O'Loughlin et al. (1980) in steep terrain in a high rainfall zone in New Zealand. These findings once more confirmed the importance of keeping soil compaction to a minimum during conversion operations.

The maturation phase

The initial changes in catchment runoff response and sediment yield associated with the early stage of a plantation become less pronounced as the new vegetation establishes itself, and these attributes usually assume stable values within 2–3 yr. However, as a result of increasing leaf biomass, both rainfall interception and forest water use (transpiration) will continue to increase, particularly until canopy closure. Certain fast-growing species, under humid tropical lowland conditions, may reach canopy closure within 3–4 yr (Lim 1988; Lugo 1992). Whilst increases in tree water use may level off when the growth rate stabilises (see Chapters 6 and 7), rainfall interception, and therefore total ET, may continue to increase as the plantation matures (Helvey 1967). In the following we will first examine the magnitude of the two principal components of evaporation, and then discuss the implications for total and seasonal water yield. Finally, the hydrological effects of various forest management practices will be treated.

Rainfall interception

There are numerous publications on rainfall interception in tropical forest plantations. However, comparison of interception data for different species and locations is complicated, not only because of potential contrasts in climatic conditions, tree growth, stand age and management history (thinning etc.) but also because of differences in methodology. In general, the amount of throughfall estimated with a 'roving gauge' method tends to be larger than that obtained with a 'fixed gauge' approach. This presumably reflects the different efficiency of the two methods in representing 'drip points' where amounts of throughfall exceed amounts of incident rainfall (Lloyd and Marques 1988). Because stemflow usually constitutes only a minor fraction of the total amount of water reaching the forest floor, it follows that the higher the throughfall, the lower the resulting interception (cf. Equation 3).

Results from what may be the most reliable interception studies (e.g. because of the use of a roving gauge technique and/or a large number of collectors plus a sufficiently long (>1 yr) observation period) for several important species used in tropical forest plantations have been collated in Tables 5.1 (hardwoods) and 5.2 (softwoods). Several important contrasts between groups of species emerge from these data.

Table 5.1 Throughfall (TF), stemflow (SF) and interception (I) fractions of incident precipitation (P) in selected hardwood plantations and natural forests in the (sub) tropics

Species	Location	Age	Tree density (ha^{-1})	TF/P	SF/P	I/P	MAP[l] ($mm\ yr^{-1}$)	Elevation (m)	Method of measuring throughfall
Fast growing hardwoods									
Eucalyptus tereticornis	India[a]	6	1660	0.81	0.08	0.12	1670	c. 700	4 fixed gauges, daily
Eucalyptus saligna	Brazil[b]	6	1685?	0.84	0.04	0.12	1280	540	12 roving gauges, daily
Acacia auriculiformis	Indonesia[c]		1010	0.81	0.08	0.11	3075	115	
		5	1010	0.75	0.07	0.18			12 fixed troughs, daily
Acacia mangium	Sabah, Malaysia[d]								
	Poor growth	4	1010[k]	0.86	?	≤ 0.14	3350	700	10 roving gauges, daily
	Reasonable growth	4	1360[k]	0.80	?	≤ 0.20			
	Good growth	4	1090[k]	0.72	?	≤ 0.28			
A. mangium	West Malaysia[e]	4 2/3	1110	0.62	0.04	0.35	2100	75	8 fixed troughs, weekly
		5 1/6	1705	0.57	0.04	0.39			Idem
Other hardwoods									
Swietenia macrophylla	Philippines[f]	15		0.79	0.01	0.20	2220	<1000?	4 roving gauges, daily
Tectona grandis	Philippines[f]	8		0.79	0.02	0.20	Idem	Idem	4 roving gauges, daily
T. grandis	Nigeria[g]	25		0.80	0.02	0.19	1200	210	5 fixed gauges, daily
T. grandis	India[h]	25		0.73	0.06	0.21	1670	700	8 roving troughs, daily
Natural forest									
Lowland rainforest	Malaysia[i]	–	–	0.81	0.02	0.17	2825	220	40 roving gauges, daily
Lowland rainforest	Brazil[j]	–	–	0.91	0.02	0.07	2475	100	36 roving gauges, weekly

[a]George (1978); [b]Lima (1976); [c]Bruijnzeel and Wiersum (1987); [d]A. Malmer, pers. comm.; [e]Lai and Salleh (1989); [f]Castillo (1984); [g]Okali (1980); [h]Dabral and Subba Rao (1968); [i]Sinun et al. (1992); [j]Lloyd and Marques (1988); [k]density at age 22 months, Sim and Nykvist (1991); and [l]mean annual precipitation

Table 5.2 Throughfall (TF), stemflow (SF) and interception (I) fractions of incident precipitation (P) in selected softwood plantations and natural forests in the (sub) tropics

Species	Location	Age	Tree density (ha^{-1})	TF/P	SF/P	I/P	MAP[o] ($mm\ yr^{-1}$)	Elevation (m)	Method of measuring throughfall
***Pinus* spp. (lowlands < 750 m)**									
P. caribaea	Brazil[a]	6	?[l]	0.90	0.03	0.07	1280	540	12 roving gauges, daily
P. caribaea[b]		13	700	0.88	–	≤0.12	1300	<500	10 roving gauges, weekly
P. caribaea	Fiji[c]	6	825	0.79	0.01	0.20	1800	115	20 roving gauges, daily to weekly
		11	820	0.77	0.01	0.22		45	
		16	620	0.82[n]	0.01	0.17		80	
P. merkusii	Indonesia[d]	9	710	0.73	0.04	0.23	2100	80	10 roving gauges, daily for 4 months
***Pinus* spp. (uplands > 750 m)**									
P. merkusii	Indonesia[e]	31	560	0.72	<0.01	0.28	2120	1375	20 roving gauges, daily
P. kesiya	Philippines[f]	10–15	704	0.84	0.06	0.11	3525	c1500	4 roving gauges, daily
P. kesiya[g]		30	?[m]	0.85	0.02	0.13	3600	1365	3 roving troughs, daily
Other coniferous softwoods									
Araucaria cunninghamii	Northeast Australia[h]	42	664	0.75	–	≤0.25	1560	760	20 fixed gauges, weekly
		42	764	0.81	–	≤0.19	2100	700	
Cupressus macrocarpa	Kenya[i]	20–25	?	0.75	–	≤0.25	2235	2650	41 fixed gauges, daily
Other softwoods									
Albizia falcataria	Indonesia[j]	5–6	600	0.82	–	≤0.18	3075	100	10 fixed troughs, daily
A. falcataria	Philippines[k]	8	?	0.77	0.03	0.20	2220	<1000	4 roving gauges, daily
Natural forest									
Submontane rainforest,	Queensland[h]	–	848	0.78	–	≤0.22	2100	760	20 fixed gauges, weekly
Montane rainforest,	Kenya[i]	–	–	–	–	0.20	2235	2850	41 fixed gauges, daily

[a]Lima (1976); [b]Lima and Nicolielo (1983); [c]Waterloo (1994); [d]Ruslan (1983); [e]C.A. Bons, pers. comm.; [f]Florido and Saplaco (1981); [g]Veracion and Lopez (1976); [h]Brasell and Sinclair (1983); [i]Pereira (1952); [j]Team Vegetation and Erosion (1979); [k]Castillo (1984); [l]original planting density 2 × 3m; [m]tree basal area $26m^2\ ha^{-1}$; [n]partly modelled; [o]mean annual precipitation

Rainfall interception by *Eucalyptus* spp. is modest at about 12% of incident precipitation, partly because throughfall and stemflow fractions are both relatively high (Table 5.1). Similar results have been obtained for natural eucalypt forests in southeastern Australia (Dunin et al. 1988; Crockford and Richardson 1990) and for plantations of *Eucalyptus camaldulensis* in a sub-humid part of southern India (Hall et al. 1992). As such, the frequently heard claim that the planting of eucalypts leads to depletion of water reserves (e.g. Vandana Shiva and Bandyopadhyay 1983) cannot be due to high interception losses. Of potential concern are the high interception losses reported for young fast-growing plantations of *Acacia mangium* in Malaysia (Table 5.1). Some of these high values may reflect the frequent occurrence of low-intensity rain (Abdul Rahim 1983), or perhaps a suboptimal sampling design, as in the example from Peninsular Malaysia (Lai and Salleh 1989). However, the results obtained by Malmer (pers. comm.) for vigorously growing *Acacia* plantations in East Malaysia (up to 28%) under high rainfall conditions are also considerable, even more so when expressed as absolute totals (up to 1150 mm yr^{-1}; Table 5.1).

Values for rainfall interception by such other widely planted hardwood species as teak (*Tectona grandis*) and mahogany (*Swietenia macrophylla*) are consistently around 20% over a range of climatic conditions (Table 5.1). Although teak is often leafless during the dry season, this is apparently more than compensated for by high interception losses during the wet season when leaf area indices may be as high as 6 m^2 m^{-2} (Grace et al. 1982). No interception data were found for *Gmelina arborea* but in view of its similarity to teak in terms of leaf area (Grace et al. 1982) and growth habit one would expect an average value of about 20% for *Gmelina* as well. The smooth bark of *Gmelina* may generate more stemflow than is found in *Tectona*, values for which are usually very low (Table 5.1); further work is needed.

Results obtained for various pine species are diverse (Table 5.2). Interception losses from rapidly growing stands of *Pinus caribaea* and *P. merkusii* were consistently above 20% of the rainfall at several lowland tropical locations (Fiji, Indonesia) but distinctly lower under more sub-humid and cooler conditions (southeast Brazil). High values (typically 25% or more) have also been reported for various coniferous plantations growing at higher altitudes not affected by frequent low cloud or fog. The latter results probably reflect a combination of low rainfall intensity prevailing at higher elevations (Calder 1990) and the high leaf area index associated with mature stands (Helvey 1967). Conversely, the low interception fractions obtained for *P. kesiya* in the mountains of the northern Philippines (0.10–0.13) may be influenced by contributions of 'occult' precipitation (mist) stripped by the trees but not recorded by the rainfall collector in the open (cf. Mamanteo and Veracion 1985). Finally, in view of its light crown, the values reported for the very fast-growing species *Albizia falcataria* seem rather high at 18%–20% (Table 5.2).

With the exception of Waterloo (1994), none of the studies quoted in Tables 5.1 and 5.2 have used above-canopy weather stations for the computation of evaporation rates from the wetted canopy in support of their traditionally-derived values of interception (cf. Lloyd et al. 1988). There is a need for more throughfall/ interception studies in tropical forest plantations that combine a rigorous design for the measurement of throughfall and stemflow (cf. Lloyd and Marques 1988) with above-canopy observations of climatic parameters. Only in this way can we expect to be able to satisfactorily separate the influence of species and stand characteristics and climatic factors on the amount of rainfall intercepted.

Transpiration

The changes in water uptake by individual trees and at stand level during different stages in the plantation life cycle, and the underlying physiological principles, are dealt with in Chapter 6. Here, the available information on annual water use by plantations (including understorey vegetation) in the humid tropics, as determined by catchment hydrological and/or micrometeorological methods, will be examined. Because most studies have produced only short-term estimates of transpiration (e.g. Whitehead et al. 1981; Grace et al. 1982; Calder et al. 1992; Roberts and Rosier 1993), the data base for annual totals is limited (Table 5.3).

Whilst there is little point in comparing instantaneous transpiration rates for different species and age classes, especially as these may have been measured under contrasting climatic and soil water conditions, a few generalisations are possible. For instance, in most young to semimature stands in lowland areas, reported daily transpiration totals are in the order of 3-5 mm whenever soil water is not limiting, regardless of species (pine, teak, young eucalypts; Okali 1980; Roberts and Rosier 1993; Waterloo 1994). Occasional peaks to 6–8 mm day^{-1} may occur under particularly favourable soil water and radiation conditions; Kallarackal 1992; Waterloo 1994). In the case of older plantations, seasonally senescing leaves or progressive moisture stress, values usually drop to 1–3 mm day^{-1} (Monteny et al. 1985; Waterloo 1994), or less under very seasonal conditions (Roberts and Rosier 1993).

To facilitate comparisons between locations, values for Et and ET in Table 5.3 have been normalised by dividing them by the corresponding open water evaporation (Penman's Eo). Few general conclusions can be drawn from Table 5.3, however, except that the water use of mature coniferous plantations often resembles that of natural forest in the same area. More work is needed, particularly in broad-leaved forests.

The widespread idea that eucalypts are voracious consumers of water was critically examined by Calder (1992). He concluded that there were large variations in stomatal behaviour and rooting patterns, and thus transpiration rates, between different species of eucalypt. Whilst certain (naturally growing) species indeed exhibited little or no stomatal control, most eucalypts did. Eucalypts are therefore likely to transpire as much as other tree species, except in situations where their roots have direct access to the groundwater table (e.g. in depressions or valley bottoms). Under such conditions, very high evaporation rates may be maintained, particularly where atmospheric demand is high (Calder 1992). Young eucalypt plantations growing in a sub-humid part of southern India showed a distinct response to both increased air humidity deficit and soil water stress (Roberts and Rosier 1993). On the other hand, transpiration rates of coppiced 5-year-old *Eucalyptus tereticornis* trees growing in a wetter part of southern India (rainfall 2000 mm yr^{-1}) increased linearly with increases in air humidity deficit during the postmonsoon season when soil water was in good supply (Kallarackal 1992). Such observations point to the need for continued studies of the water use of *Eucalyptus* under conditions of high rainfall and deep soils.

Table 5.3 Annual evapotranspiration (ET) and transpiration (Et) of mature forest plantations and selected natural forests in the humid tropics. Values have been rounded off to the nearest five units

Species	Location	Elevation (m)	ET (mm)	ET/Eo	Et (mm)	Et/Eo
Agathis dammara[a,f]	Java	600	1070	0.79	405	0.30[i]
Pinus merkusii[b,f]	Java	1300	900	0.84	445	0.42
Pinus patula[c,f]	Kenya	2400	1160	0.77	600[h]	0.41[h]
Pinus caribaea[d] 6-yr-old[g]	Fiji	80	1770[j]	1.05	1250	0.74
P. caribaea[d] 15-yr-old[f]	Fiji	230	1510	0.90	1175	0.73
Lowland rainforest[e,g]	Java	<100	1480	0.90	885	0.54
Montane rainforest[c,f]	Kenya	2400	1155	0.78	690	0.46[h]

[a] Bruijnzeel (1988); [b] C.A. Bons, personal communication; [c] Blackie (1979); [d] Waterloo (1994); [e] Calder et al. (1986); [f] catchment water balance study, values for Et derived by subtracting interception loss from total ET and hence approximate only; [g] micrometeorological methods and/or Penman-Monteith evaporation model; [h] using interception estimate by Pereira (1952); [i] low value due to high interception loss (annual rainfall 4770 mm); [j] including c. 160 mm evaporated from litter layer.

Another example of consistently high water use concerns a 6-year-old plantation of *Pinus caribaea* in Fiji (Waterloo 1994; Table 5.3). Annual transpiration by this vigorously-growing stand was about 1250 mm. Adding amounts of rainfall intercepted by the canopy (360 mm) and the thick litter layer (160 mm) brought the annual total of ET to the very high value of 1770 mm. The corresponding amount obtained for a nearby 15-year-old stand was about 1510 mm. These values constituted 82%–92% of the rainfall during the study period and one can appreciate the concern of regional water authorities over rapidly dwindling streamflow following reforestation of grassland with pines in this particular area (Waterloo 1994). This and other examples will be discussed further below.

Plantations and total water yield

As a result of the increase in ET with stand age, streamflow can be expected to decrease with time after planting. Long-term streamflow records have been collected at several locations from which changes in water yield as the stand matures can be evaluated. For example, Blackie (1979) compared the water balance of montane rainforest with that for an adjacent plantation of *Pinus patula* on deep volcanic soils at 2400 m elevation in Kenya (cf. Table 5.3). During the first three yr after planting, total annual streamflow for the pine-forested catchment remained on average about 125 mm above that for the control catchment. Results for the subsequent six yr were somewhat variable (see Blackie (1979) for explanations) but once the pines were 10–11 yr old, streamflow patterns for the two vegetation covers started to coincide. It may be concluded, therefore, that the water yield from the pine-forested catchment remained above the original value over a period of 4–10 yr. Re-analysis of the data according to the more stringent paired catchment method (Hewlett and Fortson 1983) might reveal whether this figure would be closer to the 4-year mark or to the 10-year one.

Similarly, there is evidence that ET of mature stands of *Pinus merkusii* and *Agathis dammara* in the wet volcanic uplands of Java is similar to that of natural forest (ET/Eo = 0.80– 0.84; cf. Table 5.3). It remains to be seen, however, whether this will also be the case when old-growth lowland forest is converted to fast-growing plantations. Rainfall interception (e.g. *Acacia mangium*; Table 5.1) or total water use (e.g. young *P. caribaea* in Fiji; Table 5.3) may well exceed those of natural forest (typically 10%–20% of rainfall intercepted and ET between 1300 and 1500 mm yr^{-1}; Bruijnzeel 1990).

The issue of plantation forestry vs. water yield becomes more critical in areas where rainfall distribution is seasonal, particularly so if, in addition, soils are shallow and have little opportunity to store water (Bruijnzeel 1989; Smith and Scott 1992). Under such conditions the natural vegetation consists of deciduous forest, sclerophyllous scrub or grassland, with trees usually limited to the riparian zone. Samraj et al. (1988) and Sharda et al. (1988) reported on the effect on water yield of a partial (59%) conversion of a montane grassland catchment with swampy valley bottoms (left undisturbed) to a plantation of *Eucalyptus globulus* on deep permeable soils under seasonal rainfall conditions in southern India. During the first three yr, annual water yield was hardly affected but from then onwards stabilised around a level of 120 mm yr^{-1} (or 21%) below initial values until the trees were 10 yr old.

A particularly comprehensive data set has been collected under seasonal warm-temperate conditions in the Republic of South Africa. Here, a series of paired catchment experiments has been set up since the 1930s to evaluate the hydrological effects of afforesting grass- and scrublands in different parts of the country (Wicht 1967; Bosch 1982; Van Wijk 1987; Smith and Scott 1992). Figure 5.7

summarises some reductions in annual water yield after afforestation with *Pinus patula*, *Pinus radiata* and *Eucalyptus grandis*. Several points emerge from this comparison: i) the decreases in water yield follow a sigmoidal trend; ii) the effect of afforestation with *Eucalyptus* (Mokobulaan catchment) manifests itself more rapidly than that for pines; iii) the proportion of the catchment that is afforested influences both the rate (i.e. the slope of the curve) and the amount of change (e.g. Biesevlei vs. Bosboukloof which were situated in the same area). To some extent, the contrasts shown in Figure 5.7 are due to differences in site conditions. For instance, the relatively slow response observed for the Cathedral Peak II catchment was interpreted in terms of slow forest growth under harsh conditions (Smith and Scott 1992). Also, the reductions in flow after afforestation have been expressed in comparison to the flows associated with the original vegetation, which may have differed between locations. In some areas (e.g. Mokobulaan), this was 'dry' grassland with a low water use; in others (e.g. Biesevlei and Bosboukloof) it was socalled fynbos, a tall scrub vegetation with a higher water use than grassland (Smith and Scott 1992). Nevertheless, the salient contrast between eucalypts on the one hand and pines on the other was confirmed by two other paired catchment experiments in East Transvaal (not shown in Figure 5.7; Smith and Scott 1992). Typically, the planting of eucalypts produced a response in streamflow after about three yr (cf. the findings of Samraj et al. (1988) in India), whereas afforestation with pines only did so after about five yr. Because the water use of the eucalypts tended to stabilise after eight yr (cf. Fig. 5.7), the difference between the two genera became gradually smaller with time. For example, at the relatively dry location of Mokobulaan, Smith and Scott (1992) reported that the reduction in streamflow observed 11 yr after planting *P. patula* had reached a similar level to that observed for *E. grandis* three yr previously. Because effects of afforestation on stormflows were relatively small (Bosch 1982), the changes in overall water yield were primarily manifest during the dry season (see below).

Maximum falls in annual water yield after afforestation of grasslands under South African conditions were in the order of 400–500 mm (Fig. 5.7). Recent observations in Fiji indicate that the contrast in water use between plantations of *Pinus caribaea* and *Pennisetum polystachyon* grassland approaches such high values as 700–900 mm yr^{-1} (M.J. Waterloo and L.A. Bruijnzeel, unpublished data).

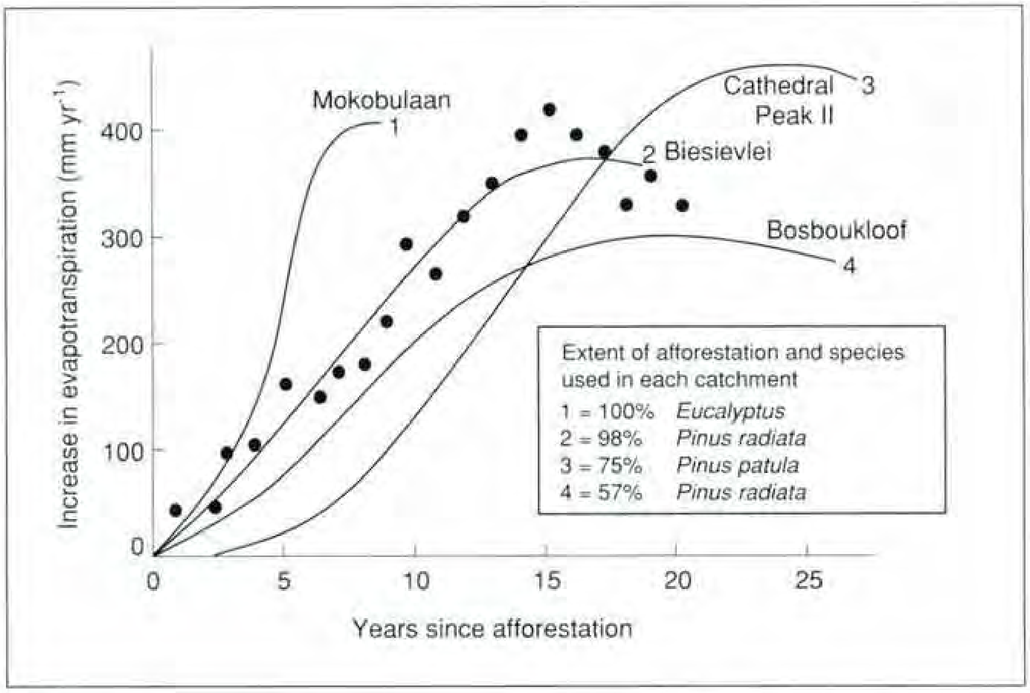

Figure 5.7 Increases in evapotranspiration with time after afforestation of grass- and scrubland in South Africa (modified from Bosch 1982). Actual data points are shown for the Biesievlei catchment only

Plantations and dry season flows

Contrasts in total evaporation between forest and grassland during wet periods mainly reflect the difference in rainfall interception between the two vegetation types (Calder 1990). During the dry season, however, the contrast in rooting depth between the two also comes into play. As a forest becomes older, the tree roots progressively reach greater depths whereas grasslands often die off during extended dry seasons and renew themselves during the next rainy season. As a result, the discrepancy in forest and grassland water use during the dry season tends to increase with age of the forest (Nepstad et al. 1994; Waterloo 1994; cf. Fig. 5.7). Therefore, depending on the vigour of the plantation, substantial reductions in dry-season water yield can be expected after afforesting grass- or scrubland. Whilst only a single study has documented the effect under humid tropical conditions (Waterloo 1994), the evidence strongly supports that obtained for warm-temperate to subtropical climates with a seasonal rainfall distribution (e.g. Smith and Scott 1992). Waterloo (1994) reported increases in dry season ET of 250–390 mm following the reforestation of fire-climax grassland in the dry zone of Viti Levu, Fiji, with *Pinus caribaea*, the actual amount depending on the age and vigour of the stand. These values correspond to a reduction in dry-season streamflow of about 50% (Waterloo 1994). In South Africa, Smith and Scott (1992) concluded that effects were noted earlier (usually after three yr) in the case of *Eucalyptus grandis* plantations than after planting *Pinus patula* or *P. radiata* (usually after about five yr). In addition, the effect turned out to be more marked for eucalypts (reductions of 90%–100%, regardless of average rainfall total or soil depth) than for pines (reductions of 40%–60%) during the first eight yr or so after treatment. However, as indicated already for total water yield, the difference—due to the different growth curves of the two groups of species—may disappear eventually, and thus the ultimate effect of afforestation on low flows may be the same, irrespective of species (Smith and Scott 1992).

At first, the experimental evidence presented above seems to contradict the deterioration in streamflow regime (increased flooding during rainy periods, reduced flow during dry spells) that is so often observed after deforestation in the tropics (Pereira 1989). The conflict can be resolved, however, by taking into account the net effect of changes in ET and rainfall infiltration brought about by the change in land use (Bruijnzeel 1989). Taking as an example a change from natural forest to degraded grassland, it will be clear that the total amount of streamflow will be much higher after deforestation (say, by 250–400 mm yr^{-1}) due to the decrease in water use associated with the transformation in cover. However, the timing of this increase in streamflow is strongly governed by the infiltration capacity of the soil. The potential surplus of water after forest removal can only manifest itself as increased baseflow during the next dry season if it has had the chance to infiltrate into the soil first. If, on the other hand, the capacity of the soil to absorb rainfall after deforestation is reduced too much by compaction or crusting, much of the water will run off down the slopes and contribute immediately to enhanced peak flows in the stream rather than percolate slowly through the soil and emerge later as baseflow. Under such conditions, dry season flows may well be reduced, despite the smaller uptake of water by the nonforest vegetation. If however infiltration capacity is maintained, the lesser water use of the new vegetation will show up as increased dry-season flow (Bruijnzeel 1989).

In view of the considerable difference in water use by seasonal grassland and actively growing forest (>250 mm yr^{-1}), the chance for increased dry-season flow after reforesting such lands is small, despite claims to the contrary (e.g. Hardjono 1980). Much depends on the ultimate rainfall-absorbing capacity following reforestation. One of the few studies that have looked at this important aspect is that by Gilmour et al. (1987) in the Middle Hills of Nepal. Gilmour and co-workers determined the saturated hydraulic conductivity of the soil under a range of conditions, viz. i) heavily grazed and trampled grassland; ii) a 5-year-old stand of *Pinus patula* on former degraded grassland; iii) and iv) 12-year-old stands of *Pinus roxburghii* on former grassland and scrubland, respectively; and v) protected natural forest. Average values of topsoil permeability increased from about 40 mm hr^{-1} (a low value) at the degraded grassland site to over 500 mm hr^{-1} in the protected forest.

When compared with the intensity of rainfall in the area, these data indicated that overland flow would actually occur on even the most degraded of sites as few as seven times a year, cf. a frequency of four times a year in the 5-year-old forest and zero occurrence in the older forests. Although topsoil infiltration capacities had improved by more than 140 mm hr^{-1}, 12 yr after reforestation, the associated reductions in surface runoff were small because of the relatively low rainfall intensities prevailing in the area. Moreover, they were much smaller than the 130–250 mm yr^{-1} of water that would be needed in this particular area to increase dry season flow (Bruijnzeel and Bremmer 1989).

It is unwise, however, to overgeneralise such findings. The interplay between rainfall and infiltration characteristics may be entirely different in other parts of the world. For instance, Patnaik and Virdi (1962) reported much lower values for saturated infiltration rates under forest and agricultural cropping elsewhere in the Himalaya. Moreover, overland flow and surface erosion may be rampant in plantations of teak (Bell 1973; Wolterson 1979), *Gmelina* and *Shorea* (particularly when subjected to grazing and regular burning), or indeed in any forest where litter is collected to serve as fuel or compost (Wiersum 1984).

Plantation Management and Hydrology

Effects of forest thinning and coppicing

The hydrological effects of thinning forest plantations are generally small and ephemeral, unless the treatment is particularly severe (>50% of basal area removed). For instance, in 25-year-old stands of *Pinus taeda* in the southern U.S., Rogerson (1967) reported an increase in relative amounts of throughfall from 77% to 94% of incident rainfall when going from a stand density of 1556 to 124 trees ha^{-1}. Storm size alone explained almost 99% of the variation in throughfall; adding stand basal area hardly increased this value. In the tropics, Veracion and Lopez (1976) and Florido and Saplaco (1981) found negligible increases in throughfall after thinning 10–15- and 30–year-old natural forests of *Pinus kesiya* in the Philippines by 30%–50% of the biomass. Significant increases were obtained, however, when 70% was removed. Similarly, Bons (pers. comm.) observed only marginal differences in throughfall in mature plantations of *Pinus merkusii* of very different stocking (240–560 trees ha^{-1}) in Java. Ghosh et al. (1980), working in broad-leaved forest (*Shorea robusta*) in northern India, applied a 20% thinning treatment and found throughfall to increase from 72% to 81%. However, because of a concurrent reduction in stemflow (from about 10% to 6% and not necessarily related to the thinning), the overall change in intercepted rainfall was a modest 5%.

It would seem, therefore, that the effect of forest thinning on rainfall interception is much less than would be expected on a pro-rata basis. This may be due to the fact that the effect of a reduction in canopy biomass is compensated to some extent by increased ventilation, and thus reduced boundary layer resistance, of the remaining trees (Teklehaimanot et al. 1991). Also, as noted by Waterloo (1994) during a study of pre- and posthurricane throughfall in *Pinus caribaea* plantations in Fiji, the effect of reduced interception by the canopy is also counteracted (typically by 1%–2%) by a concurrent increase in the amount of water intercepted by the litter layer. Not only does the latter become more exposed after the opening up of the canopy but it also has a greater biomass capable of storing (intercepting) more moisture. Another effect of thinning may be the stimulation of growth in the understorey (cf. Roberts 1983). Thus the effect of thinning on streamflow characteristics may be even smaller than that on rainfall interception.

Gilmour (1977) did not observe any changes in streamflow after selectively logging a rainforest in northern Queensland. Subba Rao et al. (1985) reported a slight increase (by 8.6%) in peak flow rates (but not in stormflow volume) in the thinning experiment in northern India already referred to. The effect had disappeared by the second year. Under sub-humid conditions the effect of thinning on streamflow will be even smaller than in areas with adequate rainfall because the remaining trees will tend to make use of the extra moisture in the soil produced by the thinning (Bosch 1979), and thus rather drastic treatments will then be needed to achieve significantly increased streamflow (Stoneman 1993).

Coppicing is such a drastic measure. The more or less complete removal of the above-ground biomass, while leaving the root system intact, will lead to high water use by trees as they rapidly redevelop their biomass. Replacing degraded scrub with *Eucalyptus grandis* and *Eucalyptus camaldulensis* in northern India produced an average reduction in streamflow (mainly stormflow) of 26% during the first five yr (Mathur et al. 1976; Mathur and Sajwan 1978). However, when the trees were coppiced, this figure rose to 68% in the first year and to 47% in the second year. The effect had disappeared by the third year after coppicing (Viswanatham et al. 1980, 1982).

Riparian zone management

The hydrological benefits of maintaining an undisturbed riparian buffer zone range from detaining overland flow from upslope areas and trapping the sediment carried by it, to keeping streamwater temperature fluctuations within acceptable limits (Clinnick 1985). Storm runoff from undisturbed forested areas in the more humid parts of the world is generated to a large extent in the near-saturated areas around streams. During storm events these 'contributing areas' may become linked to the more ephemeral elements of the stream network that act as a source of runoff to the permanent section of the stream (Ward 1984). Therefore, it is important to extend the riparian buffer zone beyond the point where regular streamflow commences and to include these ephemeral elements, even more so because the position of springheads may move upstream after forest clearing, reflecting the wetter conditions in the catchment as a result of decreased evaporation (Bren and Turner 1985). The importance of such an extended buffer zone was illustrated by O'Loughlin et al. (1980) in a study of sediment yields after clearcutting a hardwood forest in New Zealand.

The width of streamside buffer strips required for satisfactory stream protection has been a matter of debate (Clinnick 1985). Where runoff response is marked and water quality is at risk, riparian buffer strips may need to be fairly wide. This may be the case in areas with significant contributions from valley bottom SOF or from HOF generated on heavily disturbed side slopes (O'Loughlin et al. 1980; Fritsch 1993). However, when soils exhibit high infiltration rates, narrower buffers may suffice (Clinnick 1985). The recent development of powerful topography-based distributed hydrological models (O'Loughlin 1986; Moore et al. 1991) has improved our ability to predict the location and extent of surface saturation zones within the landscape for a range of climatic and pedological conditions. Pending the widespread application of such models in commercial forestry, many people consider widths of 10–30 m on either side of a perennial stream and of about 5 m around ephemeral channels sufficient (Clinnick 1985).

What are the associated costs of streamside protection in terms of water use by riparian vegetation, roots of which have ready access to the groundwater table? Dunford and Fletcher (1947) found under humid warm-temperate conditions in southeastern USA that removal of the riparian vegetation produced a decrease in the diurnal fluctuation of the baseflow but that the associated increase in water yield was not greater than would have been expected if an equal area elsewhere in the catchment had been cleared. Apparently, the riparian effect is negligible in areas where soil moisture remains readily available in all parts of the catchment throughout the year. A similar result was obtained for humid subtropical conditions in South Africa by Smith and Bosch (1989).

Minimising adverse impacts on soils and hydrology during forestry operations

There is ample evidence that the key to minimising damage to residual vegetation and soil is the careful planning, preparation and execution of a forestry operation.

Short-term economies may well be offset by the costs of restoring or maintaining productivity in the longer term. For instance, the growth of *Eucalyptus urophylla* and *Acacia mangium* trees during the first four yr after forest clearance on clayey soils by heavy equipment, windrowing and burning of slash in French Guyana and East Malaysia, respectively, was roughly half of that of trees on better-managed soils (Sim and Nykvist 1991; Fritsch 1992). In the Malaysian study the manual extraction of timber and retention of slash on-site to rot rather than burning it off, although initially more expensive than the conventional use of crawler tractors and burning of slash, proved to be more economic soon after planting. Not only was tree growth better, but also less weeding was required. In addition, adverse off-site effects such as increased catchment sediment yield (not included in the economic analysis) were lower after the more benign treatment (Malmer 1993).

Reductions in early growth might also be related to enhanced losses of nutrients due to leaching and surface erosion after the loss of the protective litter layer by the burn (Malmer 1993; Mackensen 1994) although the effect is hard to separate from that of soil compaction. Changes in soil infiltration capacity due to fire may range from negligible to considerable. Much depends on the intensity of the fire which is governed mainly by amounts and moisture content of the fuel and ambient weather conditions (Scott 1993; Mackensen 1994). Different soils may exhibit a different response to excess heat; some soil types become (temporarily) water repellent, a condition which tends to promote the generation of overland flow (Burch et al. 1989; Scott 1993). When this occurs on sites where most of the protective litter layer has just been destroyed by the fire, serious surface and gully erosion may follow (Brown 1972; Leitch et al. 1983).

Forest plantations in East Africa and Southeast Asia are often established under the 'taungya' system (Evans 1992). As the soil remains partly exposed throughout the intercropping period, the risk of soil degradation through erosion increases, particularly because taungya is often applied on steep slopes. In Java, freshly cleared fields on highly porous volcanic ash soils of sandy loam texture did not incur significant surface erosion during the first two yr of intercropping (Bons 1990; Rijsdijk and Bruijnzeel 1990) whereas in the second year coarser textured volcanic soils which were more prone to water repellent behaviour and structural decline did (Gonggrijp 1941). However, after the first year of taungya the former studies recorded intensive overland flow and erosion (up to 70 t ha^{-1} yr^{-1}) from compacted field boundaries used as footpaths. Even though the resulting gullies may stop supplying large amounts of sediment to the stream after the cessation of cultivation and the closing of the tree canopy, they may remain important as preferential routes for storm runoff. Under more marginal conditions, e.g. on the vertic clay soils often used for teak in Java, taungya may lead to heavy erosion, even to the extent that protective contour barriers of teak branches and *Leuceaena* hedgerows are destroyed (Wolterson 1979).

Without going into much detail here, the following steps and measures are generally considered essential for an operation to be successful in terms of minimising both costs and environmental damage (Marn and Jonkers 1981; Wiersum 1985; Pearce and Hamilton 1986; Adams and Andrus 1990):

I. Prelogging assessment of potentially unstable (wet depressions, very steep slopes) areas or erodible soil types; delineation of catchment boundaries and (ephemeral) drainage lines; evaluation of seasonal distribution of rainfall;

II. Preplanning of the extraction road and track network in relation to terrain characteristics, the natural drainage network, and type of logging system to be used; locating roads and log landings on ridges and away from streams and steep sections as much as possible; where unavoidable, constructing stream crossings of high standard, with access of machinery to the stream zone strictly confined to these designated crossings;

III. Timing of road construction to conform to the period of least rainfall; allowing sufficient time for earthworks to stabilise before intensive use; providing adequate drainage of roads/tracks; reducing tyre pressure of vehicles to reduce rutting of roads;

IV. Where economically feasible, using skyline systems rather than ground-based traction in steep terrain; using tracked rather than rubber-tyred machinery and restricting machine size in accordance with log weights and wetness of the soil; suspending tractor logging during very wet periods to avoid excessive compaction; minimising the number of vehicle passes by sound planning of timber extraction; yarding logs uphill rather than downhill; using winch ropes from the ridges rather than having machines clear an approach to every log; delimbing logs and leaving slash on site; limiting the burning of slash to avoid nutrient losses through volatilisation, surface erosion and leaching;

V. Maintaining buffer strips along streams (10–30 m wide, depending on slope steepness and soil erodibility) and ephemeral channels (>5 m wide);

VI. Postlogging rehabilitation of skidder tracks (removal of temporary stream crossings, construction of cross drains or bars on critical tracts) and log landings (ripping and seeding); road maintenance; grassing roadside earthworks;

VII. Between harvesting periods, maintaining an adequate ground cover to protect the soil against the enhanced erosivity of canopy drip, and limiting the collection of understorey vegetation, branches and litter for fodder, fuel or composting material.

These principles should be applied through comprehensive guidelines. Although there is a need for site-specific guidelines to take full account of local variation in climatic and soil conditions, as an interim measure tropical forest managers might do well to follow the protective guidelines developed for the extreme climatic conditions in the coastal rainforest zone of Queensland and which have proved their value (Cassells et al. 1984).

The Role of Hydrological Modelling in Plantation Management

Hydrological models may prove useful within plantation management with respect to both on-site and off-site aspects. Examples of the former include the identification of excessively wet areas, or hillslope sections having a high surface erosion or landslide hazard. Off-site aspects relate to downstream hydrological impacts of forestry operations. The close linkage between the two is demonstrated by the numerous conflicts of interest between on-site demands for water for timber production and off-site needs for irrigation, industry and urban water supply, both in the tropics (Pereira 1989) and elsewhere (Langford 1976; Calder 1990). To resolve such conflicts, sound predictions are needed of the total water use of plantations at various stages of growth, on the basis of which rational land-use decisions may then be taken (Bosch 1982).

Traditionally, foresters have relied on time-consuming paired catchment experiments to evaluate any changes in water use after plantation establishment (cf. Fig. 5.7). Whilst this approach enabled the construction of nomograms from which changes in streamflow could be read as a function of stand age and rainfall or catchment exposure in certain areas (Nänni 1970; Douglass and Swank 1975), the results were often so variable as to render their applicability for more detailed water resources planning rather limited. Curves 2–4 in Figure 5.7 illustrate the considerable variation in the change in water yield after planting scrub and grassland to pines in South Africa, both between locations and years (curve no. 2). Afforestation with eucalypts produced yet another response (curve no. 1 in Fig. 5.7). The simple 'black-box' approach of the paired catchment technique is unable to evaluate the relative importance of the respective factors underlying such differences, and this severely limits the possibilities for extrapolation of results to other areas or periods.

During the last decade considerable advances have been made in the measurement and modelling of forest hydrological and ecological processes at the local to regional scale (Running and Coughlan 1988; Shuttleworth 1988; Hatton et al. 1992; Band et al. 1993). Particularly after the arrival of dynamic physically-based and spatially distributed catchment hydrological models (O'Loughlin 1986; Moore et al. 1991), the adequate simulation of the effect on water yield of changes in catchment vegetation without the use of ample parameter optimisations has come a significant step closer. Arguably, one of the more promising model packages is the topography-driven TOPOG modelling framework whose application, amongst others, has included the successful simulation of the long-term changes in tree growth and water yield during regeneration after clearfelling a *Eucalyptus regnans* forest (Vertessy et al. 1993, 1996). However, outputs from such models are sensitive to variations in leaf area index, the rainfall interception coefficient and maximum canopy conductance, and soil hydraulic conductivity (Vertessy et al. 1993, 1996). This immediately points to the greatest problem associated with the application of advanced simulation models in the tropics, i.e. a lack of adequate input data. As a result, it is not possible at present to make reliable predictions of the effect of tropical plantations on annual and seasonal water yield in terms of tree species and age in relation to climatic and edaphic factors. However, despite the current lack of information there is reason for optimism in that the methodology to fill the major gaps in knowledge is well-established.

Pending application of the more sophisticated physically-based models to predict off-site hydrological impacts of forestry operations, tropical plantation managers will have to resort to less data-demanding yet reasonably process-based models such as ACRU (Schulze and George 1987) or PRMS (Lüllwitz and Flögel 1993). Nevertheless, there is scope for the use of the topography-driven distributed models like TOPOG for several important on-site applications that require little more input than a good contour map and basic soils information. These include the prediction of saturated zones in the landscape (O'Loughlin 1986); the spatial distribution of sheet erosion, gully erosion and landslide hazards (Vertessy et al. 1990; Dietrich et al. 1992; Constantini et al. 1993); and steady-state soil moisture distributions during wet and dry periods (Moore et al. 1988).

Synthesis

When describing the changes in hydrological behaviour of plantations at various stages of growth it is helpful to distinguish between an 'establishment phase' and a 'maturation phase'.

Upon establishing a new plantation, the soil is usually exposed for several months until a protective understorey redevelops, and during this period catchment water and particularly sediment yields, as well as peak flows, will be much increased compared to values observed previously under natural forest. The photographs on pages 159 and 160 illustrate the interaction between management and tree cover on hydrological processes under a range of forest conditions. The increases in sediment yield and peak discharges largely disappear within two to three yr, after which they assume more or less stable levels that are slightly above the original values. The increase in catchment water yield tends to last somewhat longer, usually until the canopy of the plantation closes, but information is scarce in this respect.

Relative amounts of rainfall interception after canopy closure differ between species as a function of canopy geometry and climatic conditions. Broad-leaved hardwoods such as teak and mahogany typically intercept about 20% of the rain whereas the light crowns of eucalypts intercept about 12%. Reported values for fast-growing stands of *Acacia mangium* are particularly high (up to almost 40%) whereas those for conifers are variable, but generally well under 25%. Little is known of the water use of many plantation species, particularly hardwoods such as teak, mahogany, *Acacia*, *Gmelina*, *Albizia* and *Terminalia*. To a lesser extent, this also holds true for coniferous species and (young) eucalypts. As a result, it is not possible at this stage to make reliable predictions of the effect of plantations, as the stands mature, on annual and seasonal water yield. However, there is no evidence as yet to suggest that the water use of plantations exceeds that of natural forest. On the other hand, there is increasing evidence that the planting of fast-growing trees on grasslands will lead to greatly diminished streamflow after canopy closure, particularly during the dry season. Increases in annual water use exceeding 500 mm have been reported after afforesting (sub)tropical grassland.

Despite the current lack of sound information on plantation water use there is reason for optimism in that the methodology (in terms of equipment and physically-based models) required to fill the major gaps in knowledge is well established. It is proposed that future research efforts be concentrated on the main species used in tropical forest plantations (Evans 1992) and at a relatively small number of well-researched key locations. These could be linked together in a network that captures the main features of the environmental variability encountered in the humid tropics (Bruijnzeel and Rahim 1992).

Acknowledgments

Kees Bons, Anders Malmer, Rob Vertessy and Maarten Waterloo shared unpublished data or papers. The manuscript benefited from comments offered by Drs Joe Landsberg and John Roberts. Marjolein Duifs-Eshuis assisted with the typing of Tables 5.1 and 5.2. It is a pleasure to thank Irene Sieverding for support throughout the writing of this paper and Mr H. Sion for help in preparing the figures.

Heavy erosion is often observed on poorly-drained roads, especially where erodible sub-soil is exposed in steep road sections. (Photo: T.C. Whitmore)

Where heavy machinery is employed during logging, up to 30% of the surface may be bared in roads, log landings and skidder tracks. (Photo: L.A. Bruijnzeel)

Plantations may afford excellent protection of the surface against erosion. (Photo: L.A. Bruijnzeel)

Not all forest plantations provide equally good protection of the soil against erosion. (Photo: L.A. Bruijnzeel)

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6

Dynamics of Leaf and Canopy Development

C.L. Beadle

Abstract

This chapter describes the key variables determining the dynamic nature of forest canopies. Canopies are the end result of the growth of leaves and the branches which display them and these are subject to constraints imposed by the biophysical environment. In managed plantations these constraints are often available water and nutrients, variables which are crucial determinants of canopy size through their effects on rates of canopy development and the longevity of leaves. The size and spatial distribution of the canopy are causally related to the amount of light intercepted by the leaves and this relationship is used to develop an understanding of how the productivity of plantations can be measured in terms of conversion of light energy to biomass. Accurate measures of canopy size and display are needed for such analyses and it is shown that methodologies based on leaf area to sapwood area relationships and the penetration of light through the canopy can be used in plantations. Stand production is constrained by the amount of water that is available for transpiration and data are presented to enable managers to gain a fuller understanding of patterns of demand for water by plantations and how this is related to the size of the canopy.

CANOPIES PROVIDE a dynamic link between the biophysical environment and the photosynthetic processes which convert solar energy into dry matter production and wood yield. Canopies are dynamic because of two processes. First, their size responds to changes in the physical environment as realised through episodes of leaf expansion and fall. Second, the characteristic of stand development is a progressive increase in canopy size up to and often beyond canopy closure. This is usually accompanied by changes in the display of the branches and leaves.

Canopies set limits to production. There is a linear relationship between biomass production and light interception (Cannell 1989) and the configuration of the canopy will determine the amount of light which is intercepted. In plantations, therefore, a key issue is the management of canopies to maximise interception of light throughout the rotation. Canopies also set the boundaries for the amount of water used by the stand in producing biomass, and management strategies should take into account the limits set to growth by available water. In principle, biomass production is linearly related to total water used by the canopy in transpiration.

This chapter explores the mechanisms which determine the production of the canopy and its configuration and how these are linked to light interception, production and water use (see Chapters 3 and 7). The chapter begins with a consideration of the growth of leaves and their longevity as these combine to determine the extent of the canopy. Canopy size or leaf area index is positively correlated with the rate of accumulation of biomass. In production forestry, therefore, consideration must be given to differences between species in rates of canopy development, seasonal variation in leaf area index and changes imposed by environmental stress. Accurate measures of leaf area index in a dynamic system are an inevitable challenge. Two approaches are considered, one based on the ratio of leaf area to sapwood area, the second based on the penetration of light through the canopy.

A particular task of this chapter is to provide a full understanding of our current knowledge of how light interception impinges on biomass production. The variables of interest are the vertical distribution of foliage which defines the volume and depth of the canopy, and the display of the leaves as determined by the angular distribution of the branches and of the leaves themselves. The resulting spatial distribution of leaves is described in light interception models by a key parameter referred to as the foliar absorption coefficient.

The management of plantations for optimum use of available water requires a precise knowledge of the patterns of supply of and demand for water throughout the course of the rotation. The final section deals with this issue in the context of relationships between water use and stand production and how these relate to the size of the canopy. Available water is that portion of rainfall which is stored in the soil profile and used in transpiration. Interception loss (see Chapter 5) is rainfall which is directly evaporated back to the atmosphere from the surfaces of the stand and is, in effect, water foregone to production.

Plantations established in the tropics include exotic species from the genera *Acacia*, *Eucalyptus* and *Pinus* (Chapter 1). Many of the principles discussed in this chapter have been established from related species in different climatic zones. While this wealth of information provides a foundation for studying canopy development in the tropics, species native to tropical environments often have patterns of growth quite different from those of the introduced species and those from other climatic zones. Wherever possible, attempts have been made to demonstrate the relevance of principles and relationships to tropical environments.

Leaves

Leaves vary considerably in size and shape. There are well-defined differences in the period of time that they remain functional. Size and longevity are both subject to change under environmental stress. The basic properties of leaves which relate to their expansion and retention determine the extent of the canopy at any time.

Leaf growth

Leaves grow by expanding their surface area and increasing their mass. Their potential for expansion is determined by the extent of cell division and their size by the capacity of those cells to expand. When water and nutrient supplies are adequate, a major variable determining growth is air temperature above a minimum critical temperature. Rates of leaf expansion increase linearly above that critical temperature until an optimum temperature is reached and subsequently decline (Monteith 1981). As a consequence, leaves may not reach maximum size if periods of expansion coincide with subcritical temperatures. In the humid and dry tropics, temperatures are maintained within well-defined limits (Chapter 3) but are moderated and reduced by altitude and levels of cloud formation. Variation in leaf size was better explained with mean annual temperature than with precipitation and evaporation along environmental gradients in forest in Costa Rica (Dolph and Dilcher 1980).

Cell division and the emergence of leaves have a large demand for assimilate but these processes are relatively insensitive to stresses arising from declining levels of available water and nutrients. Cell expansion also involves synthesis of new materials but demand for new assimilates is low while that for nutrients is high (Kriedemann 1986). Expansion is also a function of turgor (P) and quite sensitive to water stress (Bradford and Hsiao 1982).

Growth requires an irreversible increase in cell volume (V). A threshold value of turgor, referred to as the yield turgor (P_y), defines the point when irreversible expansion commences. The rate of expansion (dV/dt) can then be defined as a function of the difference between P_y and P, the growth-effective turgor ($P- P_y$), and a variable (ϕ) describing the extensibility of the cell wall (Lockhart 1965). Diurnal patterns of leaf extension (change in length per unit time, dL/dt) of *Salix viminalis* were observed to be in phase with $P- P_y$ (McDonald and Stadenberg 1993). Extension growth of *S. viminalis* was also correlated with diurnal changes in temperature and point to temperature-dependent processes, perhaps related to wall loosening and changes in ϕ, controlling dL/dt (McDonald et al. 1992). Acidification of the cell wall space is required for wall loosening and is driven by light (van Volkenburgh et al. 1985). The control of leaf expansion is complex but it would appear that the growth of leaves is also mediated by light and temperature in tropical species (Longman and Jenik 1974).

If the growth-effective turgor falls to zero, leaf expansion will cease. Leaf production and leaf expansion of *Eucalyptus globulus* and *E. viminalis* were reduced by water stress and this was associated with significant reductions in predawn (ψ_{max}) and midday water potentials (Metcalfe et al. 1989; Phillips and Riha 1994). In *Theobroma cacao*, final leaf area could be predicted by an expression of cumulative water stress (Joly and Hahn 1989). A useful measure of cumulative water stress is the water stress integral (S_ψ). This index integrates stress in terms of periodic measurements of ψ_{max} below a threshold value of ψ_{max}, the threshold defining the commencement of the effects of water stress on growth (Myers 1988). Using this approach, dL/dt of needles of *Pinus radiata* over a range of water and nutrient treatments was found to be negatively and linearly correlated with S_ψ over monthly periods: dL/dt was less sensitive to S_ψ at the end compared to the beginning of the growing season (Fig. 6.1, Raison et al. 1992a).

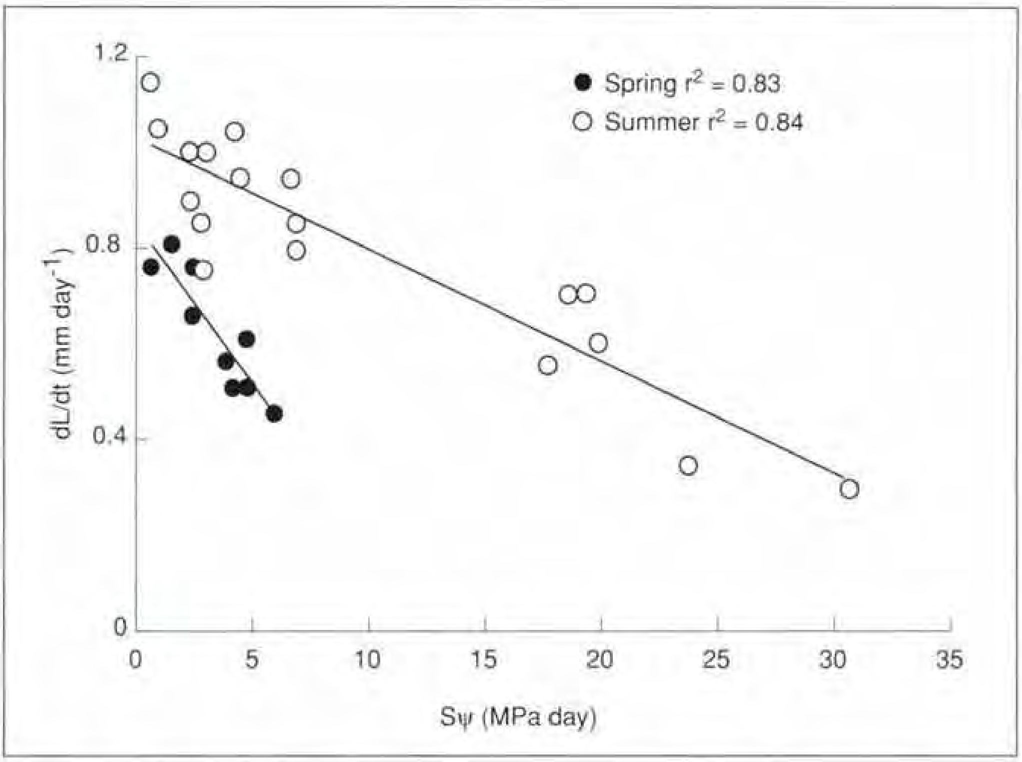

Figure 6.1 Leaf extension (dL/dt) of *Pinus radiata* expressed as a function of water stress integral (S_ψ). The observations are derived from a range of fertilizer and irrigation treatments applied over a four-yr period. Note that dL/dt was less sensitive to S_ψ at the end (summer) compared to the beginning (spring) of the growing season (adapted from Raison et al. 1992a)

Nitrogen (N) has a large effect on the development of leaves. In *S. viminalis*, significantly higher dL/dt and final leaf size were observed in leaves receiving a high N treatment compared to those receiving a low N treatment (Stadenberg and McDonald 1994). As there were no consistent differences in turgor between treatments and consistently higher values of ϕ in the high compared to the low N treatment, the effects of N were probably associated with greater cell wall loosening and enlargement at a given value of $P-P_y$. The importance of foliar levels of N as a determinant of final leaf size was also demonstrated for *Gmelina arborea*: rates of leaf expansion, however, were more sensitive to foliar levels of phosphorus (Cromer et al. 1993b). In *P. radiata*, levels of nitrogen deficiency in needles contributed to a four-fold variation in final length through their effect on ψ_{max} and S_ψ (Raison et al. 1992a).

The period as well as the rate of expansion of leaves can vary considerably within and between species. Needles of *P. radiata*, depending on environment, attained maximum extension in four to seven months though this maximum and dL/dt increased and the time taken to reach 95% elongation decreased with increasing height in the canopy (Raison et al. 1992a; Whitehead et al. 1994). In *Eucalyptus nitens* and *Eucalyptus delegatensis* leaf expansion was completed within about three months while temperatures were favourable for growth but the period of expansion and final leaf size were reduced at the end of the growing season when low temperatures limited growth (Beadle and Turnbull 1986). Rates of leaf extension in some tropical species can be as high as 18 mm day^{-1} and growth can be completed within 15 days (Longman and Jeník 1974; Shukla and Ramakrishnan 1984). Such differences relate to leaf longevity which often reflects patterns of growth and levels of stress experienced by species in their native habitats.

Leaf longevity

Leaf longevity (life span of leaves) is the period that a leaf remains functional between initiation and fall. Species and environmental variables affect longevity (Reich et al. 1992; Gower et al. 1993). In the context of stand physiology of plantations, a major interest is to determine how leaf longevity affects fluctuations in the extent of the canopy. However, the activity of leaves across a range of species is closely related with their longevity. For example, the five-yr life span of needles of *Picea abies* resulted in a two to three times greater CO_2 uptake compared to that of a deciduous leaf of *Fagus sylvatica* in one growing season (Schulze et al. 1977).

Leaf longevities vary by up to three orders of magnitude between species. At one extreme is the slow-growing long-lived *Pinus longaeva*, the bristle-cone pine with a life span of leaves of up to 45 yr (Ewers and Schmidt 1981) and at the other, early successional rainforest species with high turnover rates and a life span as short as 50 days (Shukla and Ramakrishnan 1984). There are, surprisingly, few studies of leaf longevity in plantations. From those reported (Table 6.1), it can be seen that conifers have longer life spans than evergreen broadleaves, like *Eucalyptus*. Life spans of temperate deciduous species are largely dictated by the length of the growing season.

Table 6.1 Character and life span of leaves in some plantation species

Species	Location	Leaf character	Life span (yr. months)	Reference
Eucalyptus	Portugal	Broadleaved evergreen	3.0	Cannell (1989)
Leucaena leucocephala	Philippines		0.2–0.4	Kanazawa and Sato (1986)
Quercus rubra	USA—Wisconsin	Broadleaved deciduous	0.5	Gower et al. (1993)
Picea abies	USA—Wisconsin	Coniferous evergreen	5.6	Gower et al. (1993)
Pinus resinosa	USA—Wisconsin		3.1	Gower et al. (1993)
Pinus strobus	USA—Wisconsin		3.0	Gower et al. (1993)
Picea sitchensis	Scotland		3.0–8.0	Ford (1982)
Larix decidua	USA—Wisconsin	Coniferous deciduous	0.6	Gower et al. (1993)

For tropical species, leaf longevities are typically short but may extend to 18–20 months in upper montane forest (Grubb 1977). Early successional species have a high turnover and an evergreen or leaf-exchanging (continuous leaf production and fall) pattern. Conversely, late successional species have a slow turnover and are deciduous (Shukla and Ramakrishnan 1984). The canopy dynamics of tropical species in plantations have received little attention. In one study, in *Leucaena leucocephala* which grows without dormancy in Mindanao Island, Philippines, mean life span of leaves in stands of the same age at three sites varied between 1.7 and 3.5 months and was directly proportional to the mean leaf mass of the stand. The high turnover of leaves, seven times per yr at the poorest site, was associated with a very low stem volume increment (Kanazawa and Sato 1986). In this species a disproportionate amount of carbon is allocated to maintain a small canopy and plantations are suited only to sites with adequate supplies of water and nutrients.

Levels of available water modify leaf longevity. In *P. radiata*, needles were retained for up to five yr in open stands with low levels of water stress but this was reduced to two yr as levels of stress increased and induced significant loss of foliage. Monthly needle fall was positively correlated with the water stress integral, S_{ψ}, during the same month (Raison et al. 1992b). In tropical deciduous species, leaf longevity is strongly seasonal and largely determined by the levels and intensity of water stress experienced at the site. Interruption of the drought cycle by rainfall or irrigation in *Tabebouia neochrysantha* led to immediate budbreak and leaf expansion, and canopy recovery was completed in two weeks (Borchert 1994). Nutrition also modifies longevity. Application of N to *Pinus contorta* in Scotland increased longevity (Miller and Miller 1976). In contrast, neither application of fertilizer, including N, nor weed control had any significant effect on needle longevity of *P. ponderosa* in Florida, USA (Dalla-Tea and Jokela 1991).

Leaf longevity is associated with adaptation to drought and low temperature. Plants with a long life span of leaves can minimise investment in new foliage but require leaves which are suited to survival. Studies in tropical forests have shown that such leaves are structurally and chemically more robust in order to deter herbivory, and physiologically slower in respect of photosynthetic and transpiration rate (Coley 1988; Reich et al. 1991). Maximum rates of photosynthesis expressed as a ratio of leaf dry weight and leaf N were inversely related to longevity (Gower et al. 1993). Specific leaf area (SLA, the area of the leaf as a ratio of its dry weight) was also inversely related to longevity (see also Reich et al. 1991) and its value as an indicator of longevity in plantation species is worth exploring.

Leaf Area Index

The size of a canopy at any one time is defined by its leaf area index (L^*), the leaf area (A_l) per unit land area. L^* is effectively a measure of the leafiness of the stand and influences productivity through interception of light. The establishment and management of plantations should be based on an understanding of the development and maintenance of canopies. In general L^* that can be maintained at a given site will be determined by the level of available water and nutrients. Silvicultural practices may modify these levels to increase L^* and the potential productivity of the site. In principle, the aim of management should be to optimise the conversion of light energy to biomass or wood yield throughout the life of the crop. The relevant issues are the species, its pattern of canopy development and the dynamics of L^*.

In many reports, the basis for measuring L^* is not stated and care should be taken when making comparisons between experiments. In this chapter, A_l is described as the projected area, which best describes the area available for interception of incident light. For broad-leaved species, projected area is the area of one side of the leaf. In the literature total surface area ($2A_l$) is often used for such leaves. For conifers, which have needles with a three-dimensional shape, total surface area will exceed $2A_l$.

Species and canopy size

A species will attain maximum L^* under optimum conditions for growth and for closed canopies, maximum L^* will be related to the ability of the lower leaves in the canopy to intercept sufficient light to maintain a positive carbon balance. Otherwise these leaves senesce and fall.

There is inadequate data to consider how canopy size varies between species. Published values are usually based on a single set of measurements made on one occasion and it is not always possible to conclude whether these values represent a maximum or are for closed canopies. Despite these limitations, values for plantations across a range of species in contrasting environments are presented (Table 6.2).

We have seen in Chapter 3 that, given simple assumptions about the distribution of foliage and the interception of light, 95% interception by canopies will occur when L^* is 6. It is apparent from Table 6.2 that canopies of all species can exceed this value, including those of deciduous forest in the tropics (*Tectona grandis*, Nwoboshi 1983). Deciduous forest periodically renews its entire complement of leaves and the energy expended for this renewal may limit the development of large canopies (Cannell 1989), but there are exceptions. Two hybrid clones of *Populus trichocarpa* × *Populus deltoides*, had L^* of 11.2 and 11.6 respectively (Table 6.2, Ceulemans et al. 1988). These very large canopies, possibly the highest reported for deciduous plantations, were attributed to an efficient branch arrangement and leaf display. Nonrandom distribution or grouping of foliage and more vertical orientation of the leaves ($k<0.5$, see Equation 1, Chapter 3) will increase the amount of foliage required for 95% light interception and the maximum L^* achievable.

Large canopies are more prevalent in some types of coniferous forest, but not all. Large canopies are probably related to grouping of foliage that allows better penetration of light deeper into the canopy and to a capacity for retaining foliage at the bottom of the canopy at low levels of incident radiation. Leverenz and Hinckley (1990) investigated twelve conifers with maximum L^* from 3.5 to 20. Variation between species was correlated to the morphology of the shade-adapted shoots (see Fig. 6.2). There is a dearth of information on L^* of coniferous plantations in the tropics though one report showed that maximum L^* of 10- to 15-yr-old *Pinus caribaea* on grassland sites in Fiji varied between 3.5 and 4 (Waterloo 1994). *Pinus* species are typically at the lower end of the range of L^* for conifers.

Several estimates of L^* are available for eucalypts (Table 6.2). In plantation forestry, the preferred species are from the subgenus *Symphyomyrtus*. These are characterised by high early growth rates (Turnbull et al. 1993) and their canopies respond vigorously to silviculture designed to improve water and nutrient supply. For *Eucalyptus grandis*, maximum L^* was 4.5 in a plantation in subtropical South Africa (Dye and Olbrich 1993), 5 in a fertilised plantation in subtropical Australia (Cromer et al. 1993a) and 6.5 in an effluent-irrigated plantation in a Mediterranean climate with cold winters, also in Australia (Myers et al. 1996). For *E. globulus* and *E. nitens*, maximum L^* was 8.3 and 6.1, respectively, in an irrigated and fertilised plantation in a cool temperate climate in Tasmania, Australia (White 1996). In

Table 6.2 Examples of leaf area index (L*) across a range of broadleaved and coniferous plantations

Leaf character	Species	Location	L*	Reference
Broadleaved				
	Eucalyptus grandis	Australia—Queensland	5.2[a]	Cromer et al. 1993a
	E. grandis	Australia—New South Wales	6.5[a]	Myers et al. 1996
	Eucalytpus globulus	Portugal	3.8	Gazarini et al. 1990
	E. globulus	Australia—Tasmania	8.9[a]	White 1996
	Eucalyptus nitens	Australia—Tasmania	6.9[a]	Roberts et al. 1992
	Eucalyptus camaldulensis	India—Karnataka	2.3	Roberts et al. 1992
	Eucalyptus tereticornis	India—Karnataka	2.2	Roberts et al. 1992
	Leucaena leucocephala	Philippines	5.5	Kanazawa and Sato 1986
	Hevea brasiliensis	Ivory Coast	4.3	Monteny et al. 1985
	Populus hybrid	USA—Washington	11.6[a]	Ceulemans et al. 1988
	Quercus rubra	USA—Wisconsin	4.5	Gower et al. 1993
	Salix viminalis	Scotland	4.5	Cannell 1989
	S. viminalis	Sweden	6.5	Eckersten 1984
	Tectona grandis	Nigeria	6.7	Nwoboshi 1983
Coniferous				
	Pinus caribaea	Fiji	4.4	Waterloo 1994
	Larix decidua	USA—Wisconsin	5.1	Gower et al. 1993
	Picea abies	USA—Wisconsin	10.2	Gower et al. 1993
	Pinus resinosa	USA—Wisconsin	6.2	Gower et al. 1993
	Pinus strobus	USA—Wisconsin	7.4	Gower et al. 1993
	Pinus radiata	Australia—ACT	8.0[a]	Raison et al. 1992b

[a] L* stated was the maximum recorded

contrast, maximum L^* of a plantation of *E. globulus* being managed for maximum growth through regular irrigation with nutrient solution in a warm Mediterranean climate in Portugal was only 3.8 (Gazarini et al. 1990). In a monsoonal climate in south India, maximum L^* was apparently just 2.4 and 2.2 in *E. camaldulensis* and *E. teretecornis*, respectively (Roberts et al. 1992).

A tentative conclusion from the above is that, in some eucalypts, maximum L^* attained is lower in warmer compared to cooler climates. In climates with high levels of incident radiation, and where temperature rarely limits growth, we can hypothesise that canopy photosynthesis may be optimised at lower L^* such that the amount of carbon allocated to stem compared to leaf biomass is higher than in cooler climates where potential productivity is relatively lower (White 1996).

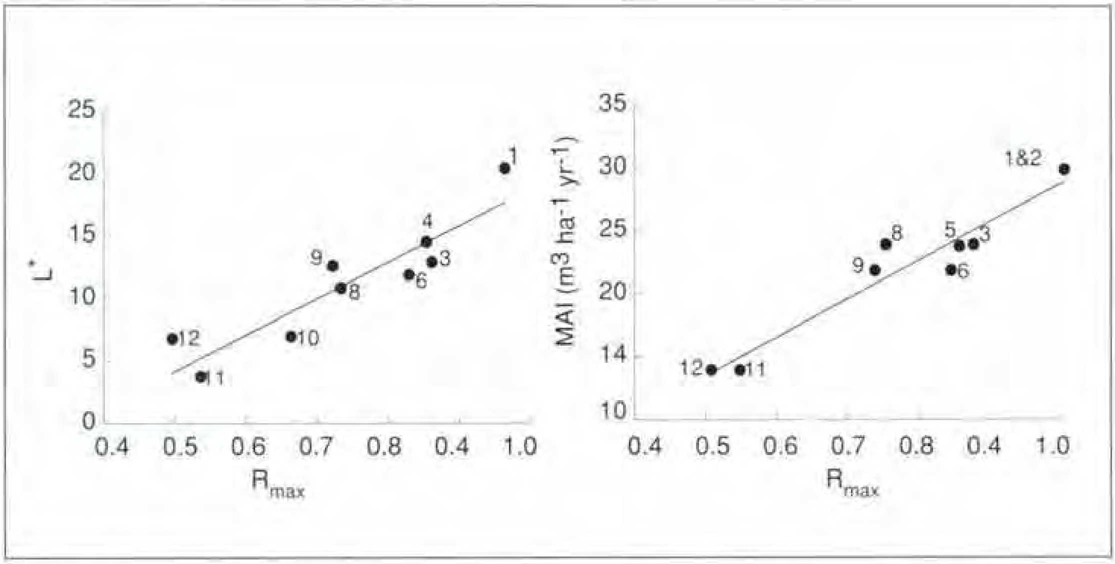

Figure 6.2 The relationships between leaf area index (L^*) or mean annual increment (MAI) and maximum silhouette-area ratio (R_{max}, see p. 183) of current-year shoots in the lower canopy of conifers. These relationships illustrate the importance of shoot structure on the interception of light by the canopy. The numbers represent a range of species and L^* is close to the maximum for that species (adapted from Leverenz and Hinckley 1990)

Canopy development

The relationship between L^* and stand age depends on species, site, and water and nutrient availability. There are few time-series studies which demonstrate how L^* changes with stand age (or seasonally). In general, L^* increases to a maximum as the stand develops and then falls or is maintained at some equilibrium value for an extended period (Jarvis and Leverenz 1983). Cromer et al. (1993a) showed that this maximum can be achieved in about 12 months in heavily fertilised plots of *E. grandis*. In young stands of *E. globulus* and *E. nitens*, on sites well supplied with available water and nutrients, rates of development of L^* were inversely related to the altitude of the site: maximum L^* of *E. globulus* occurred at age 3 yr and of *E.*

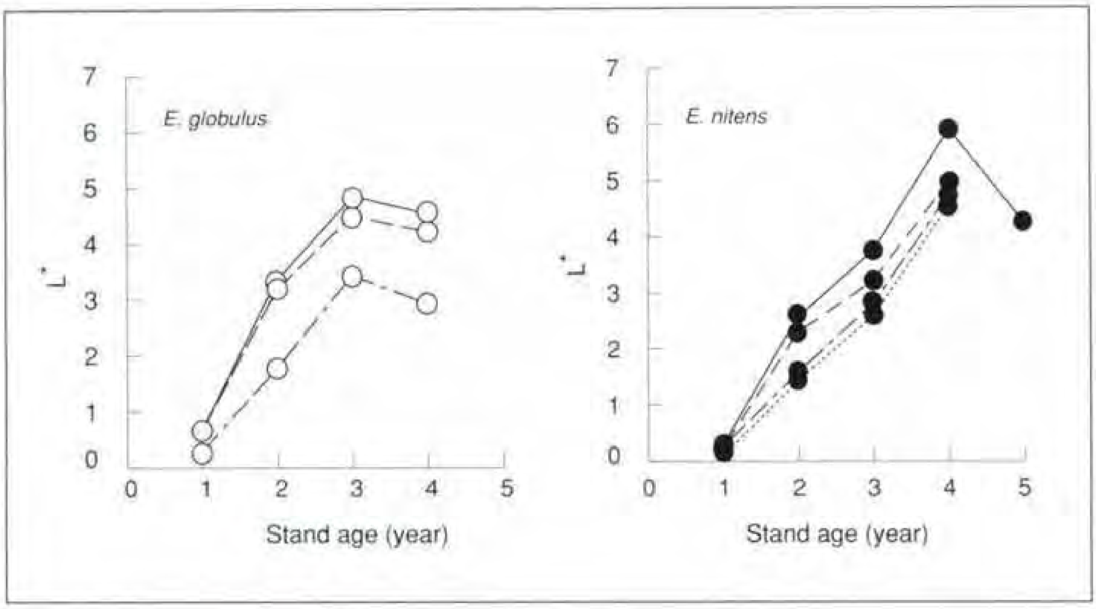

Figure 6.3 Canopy development of *Eucalyptus globulus* and *E. nitens* at four sites (—— 60 m; – – 240 m; – ·, 440 m; ······· , 650 m). Note the faster development of *E. globulus* and the decrease in L* after canopy closure (adapted from Beadle et al. 1995)

nitens, at the warmest site, at age 4 yr (Fig. 6.3, Beadle et al. 1995). The ranking of L* showed that the length of the growing season declined with altitude as the integrated thermal time above a critical temperature decreased.

The rate of canopy development in conifers is slower than that in broad-leaved species. This is partly because conifers have lower net photosynthetic rates and larger specific leaf weights which reduce the amount of light intercepted per unit of projected area. The small area of needles also requires investment in numbers of primordia which are between one and two orders of magnitude greater than required to develop a similar leaf area in a broad-leaved species (Cannell 1989).

All forests exhibit seasonal variation in L*. In strongly seasonal temperate climates this is to a large extent a function of temperature. In tropical and subtropical environments rainfall patterns will probably be the major determinant. Net increases in L* will occur during periods of leaf expansion and net decreases during periods of marked litter fall. Inter-annual as well as seasonal variation will also be observed in response to variable levels of water and nutrient stress. For example, L* of closed stands of *Pinus elliottii* in the southeastern United States varied seasonally between 40 and 50% (most of this variation was associated with the period of leaf expansion) and by a factor of 2 over a three-yr period (Gholz et al. 1991) . In a subtropical dry forest in Puerto Rico, L* varied seasonally between 1.2 and 4.2 (Lugo et al. 1978). Seasonal variation will be higher if periods of maximum leaf production are out of phase with periods of maximum foliage loss as observed in *P. radiata* in Australia. Increases in foliage mass of between 2 and 6.5 t ha^{-1} were recorded in a range of treatments between the end of the winter minimum and the maximum at the end of the summer. These were equivalent to changes in L^* of approximately 1.1 and 3.0, respectively (Raison et al. 1992b).

The effect of levels of available water on L^* of two eucalypt species is shown in Figure 6.4. Water stress reduced the rate of development of L^*. There was also a difference between species. As the degree of seasonal drought stress increased, the differences between L^* of the irrigated and rainfed treatments of *E. nitens* increased: for *E. globulus*, there was little effect until severe stress caused the cessation of leaf area development in the rainfed treatment. Under prolonged drought, eucalypts shed leaves. Loss of leaf area is a mechanism for reducing transpiration and leaf fall may occur over a number of months during a sustained drought but canopies recover readily after rainfall (Pook 1985). Conversely, irrigation (and fertilizer) increase the total number and size of leaves produced (Pereira et al. 1989). Significant loss of foliage also occurs in conifers under water stress (Raison et al. 1992a, b). As the number of foliar initials is reduced during such periods (Bollman et al. 1986; Cremer 1992), potential L^* is also reduced during the season of expansion. The continued availability of water is critical to the long-term retention of leaf area. This was illustrated by Gholz (1982) who showed that L^* of a range of forest communities along gradients of precipitation and pan evaporation was linearly related to a simple index of soil water balance during the growing season.

Leaf area index is also positively correlated to the nutritional status of the site (Hedman and Binkley 1988). Forest fertilisation, especially application of N, results in large increases in L^* (Nambiar 1990; Cromer et al. 1993a; Heilman and Xie 1994). The effects of fertilizer are often increased by concurrent weed control. In *Pinus taeda* and *P. elliotti*, fertilizer and weed control increased L^* >1000% and led to a significant acceleration of canopy development (Colbert et al. 1990; Dalla-Tea and Jokela 1991). Interaction between the effects of fertilizer and weed control on growth and canopy development in plantations is sometimes observed (Waring and Snowdon 1985). This occurs because fertilizer enhancement is achieved only when weeds are adequately controlled. Otherwise the weeds compete effectively for the nutrients and reduce the positive effects of fertilizer. Competition for water and nutrients often occurs simultaneously, contributing to this effect.

Canopy Structure

Vertical distribution of foliage

The vertical distribution of foliage changes with stand age, the most marked change occurring at canopy closure as the amount of available light at the canopy base falls below light compensation point. In general, branches will remain live and foliage will continue to develop and be retained longer in young or open-grown stands. At

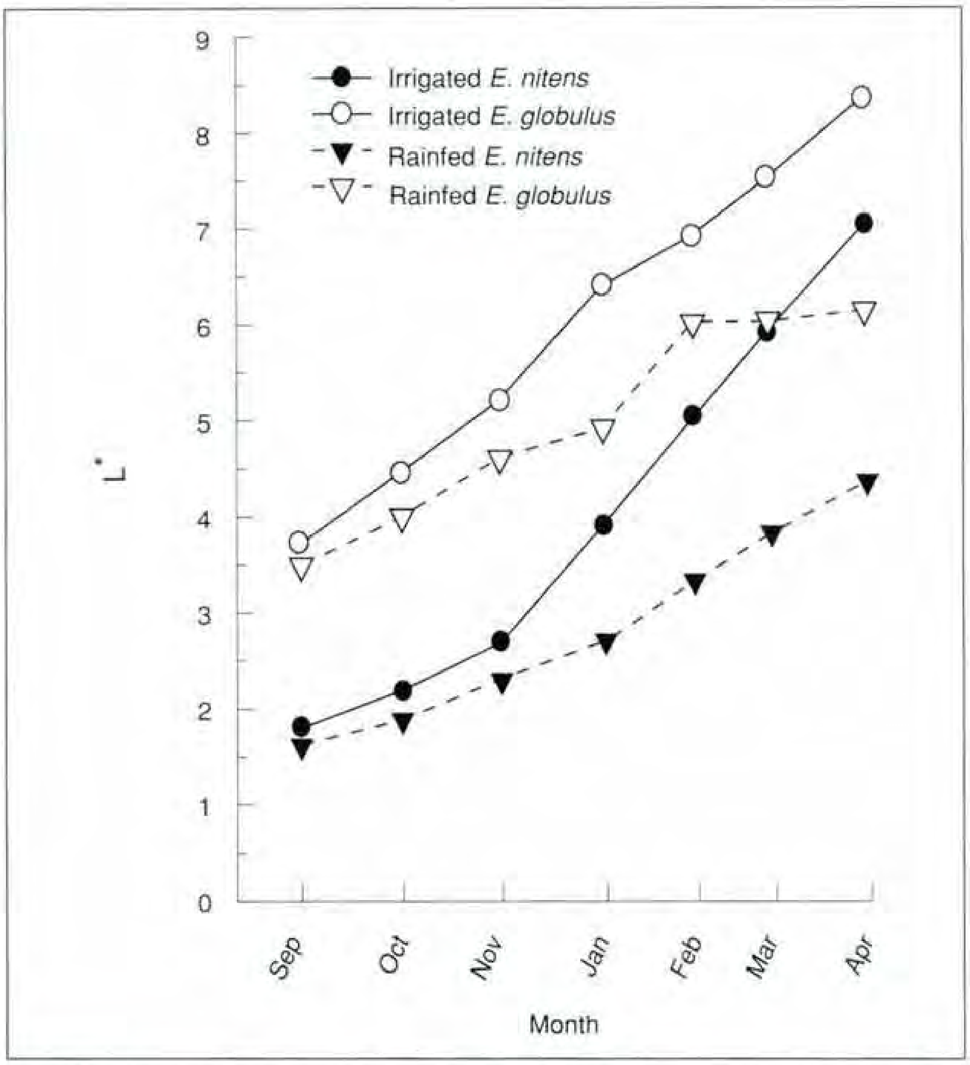

Figure 6.4. The effects of water stress on leaf area index (L*) of eucalypts in plantations. The figure shows the development of L* during the third growing season in irrigated and rainfed treatments of *Eucalyptus globulus* and *Eucalyptus nitens* in Tasmania, Australia (adapted from White 1996).

canopy closure and beyond, there is a redistribution of foliage which may differ considerably between individual trees but take on a particular distribution at canopy level. For both open and closed canopies, the crown is distributed more evenly in space in coniferous than in broad-leaved species.

In conifers with closed canopies, foliage in the vertical plane is distributed approximately symmetrically on either side of the midpoint of the canopy. Data on crown profiles are fitted to statistical distributions, commonly the *normal* function (Jarvis and Leverenz 1983). For some cases, there may be skewness upward or downward from the midpoint (e.g. Beadle et al. 1982; Hashimoto 1991). In others, vertical distribution of dry weight may be approximately *normal* while that of leaf area may be skewed downwards (Gary 1976) as the specific leaf area increases with depth in the canopy . If skewness (or kurtosis) is significant, this can be dealt with by including appropriate parameters in the *normal* function. In species which accumulate more foliage area after canopy closure, upward movement of the canopy may lead to an increase in canopy depth.

At the level of individual trees, foliage distribution in conifers may be bimodal or trimodal (Beadle et al. 1982). One possible explanation for modality may be annual variation in internode length, differences in branch elongation patterns or an uneven arrangement of branches within the canopy. An uneven arrangement may possibly result from the presence of large branches (Osawa 1990) and greater exposure— to light or to wind—on the sides of some trees compared to others. An alternative statistical model, the Weibull distribution has been used to describe the arrangement of foliage on individual trees. This function incorporates scale and shape factors which have been observed to change systematically as a function of tree size in *Chamaecyparis obtusa*. Crown profiles are constructed from the distribution of individual tree profiles in the stand (Mori and Hagihara 1991).

The distribution of foliage in closed broad-leaved forest is quite variable though in some studies normal and skewed-normal distributions have been observed (see Jarvis and Leverenz 1983). *E. globulus* had a maximum amount near the midpoint of the live crown (Pereira et al. 1987). In *Nothofagus solandri*, the distribution was approximately bimodal with foliage concentrated at the top of the canopy and a second peak within the mid-canopy (Hollinger 1989). Displacement of mean canopy depth may occur if a large proportion of either dominant or suppressed individual trees occupy the stand (Stephens 1969). Thinning a closed stand will lead to a redistribution of leaf area as leaf production at the base of the canopy is stimulated by increased levels of available light (Bidlake and Black 1989). Application of fertilizer before crown closure may also increase leaf area in the middle and lower crown (Vose 1988). However, while site differences in the level of available water and nutrients are strongly associated with total leaf area, clear patterns in the distribution of foliage with measures of soil fertility are not observed (Hedman and Binkley 1988).

In developing or open stands, foliage may increase from the apex downwards and this pattern may be retained until canopy closure (Hashimoto 1991). In irrigated stands of *E. globulus* and *E. nitens*, the mean proportions of leaf area in the upper, middle and lower third of the canopy by depth were, respectively, 0.13, 0.39, 0.48 at age two yr, and 0.11, 0.36, 0.53 at age three yr just prior to canopy closure (White 1996). The vertical distribution of foliar nutrients may differ from that of leaf area. In *E. grandis* at age 6 months, N and P concentrations increased radially from the base of the tree: by age 16 months, around canopy closure, the highest concentrations were observed in the upper canopy (Leuning et al. 1991a). Trees in more open stands can have increased orders of branching and longer-living branches compared to those in closed stands (Rook et al. 1987).

Branch, foliage angle and grouping of foliage

The arrangement of foliage and branches throughout the canopy determines structure. Structure determines penetration of light through the canopy and the distribution of microenvironmental factors such as leaf and air temperature, vapour pressure deficit and windspeed. All canopies are complex and a precise description of the impact of orientation and arrangement of foliage on the above variables is usually not attempted. Instead, the assumption is commonly made that leaves are distributed randomly in space and that leaf inclination angles are spherically distributed. This has proved particularly useful for evaluating the penetration and interception of light by plant canopies (see below and also Chapter 3).

The arrangement of branches may also take a well-defined form and it is not uncommon for branch angle to the horizontal to decrease with depth in the canopy. There was no preferred azimuthal distribution of individual shoots in young stands of *Pinus sylvestris* and in larger trees a spherical distribution was a good approximation of shoot orientation (Stenberg et al. 1993). Leaf inclination angles may also decrease with depth in the canopy in both single and mixed-species stands (Hutchison et al. 1986; Hollinger 1989). Such an arrangement allows greater penetration of light to the base of the canopy and a more even distribution of light.

The structure of shade-adapted shoots in the lower crowns of coniferous species has been shown to have important consequences for their leaf area index and productivity. The maximum silhouette-area ratio of these shoots is a measure of their capacity to intercept incoming radiation and to maximise photosynthetic efficiency. The ratio (R_{max}) is defined as the area of a silhouette of an intact shoot divided by the projected area of detached needles. In principle the ratio will not exceed 1.0, a condition in which the needles are flat and there is no self-shading when the shoot is illuminated normal to its broadest dimension. Figure 6.2 shows that maximum L^* and maximum mean annual increment of a range of conifers are strongly correlated with R_{max} of the current-yr shoots in the lower canopy, that is, a large canopy size and high photosynthetic production are associated with more effective interception of light at the base of the canopy (Leverenz and Hinckley 1990). The silhouette ratio is effectively a surrogate for the extinction coefficient (see below) of the lower canopy. The inverse of this ratio has been measured more extensively through the canopy as a means of expressing the degree of grouping or clumping of foliage.

The structure of many canopies is not random but rather the foliage is grouped (or clumped) into whorls and into shoots allowing better penetration of radiation into the canopy (Norman and Jarvis 1974; Oker-Blom and Kellomäki 1981). Canopies with grouped foliage can achieve higher levels of L^* for a given level of light interception. It is often reported that coniferous canopies have a greater level of grouping compared to broad-leaved canopies.

The degree of grouping of foliage can vary significantly between individual trees in the same stand. In *Pinus radiata*, the fraction of crown volume, expressed as an array of 10^{-3} m^3 cells, occupied by foliage varied from 0.08 to 0.23 and this was related to the degree of development of third-order branches. This degree of clumping increases penetration of beam radiation to such an extent that assuming random distribution of foliage would have overestimated interception by up to 30% (Whitehead et al. 1990). Grouping can also occur at the level of individual trees as occurs in row crops or in forests before canopy closure.

Leaf Area and Sapwood Area

Leaf area index can be measured or estimated directly or indirectly. Indirect techniques are considered in the next section. Direct estimates can be made from litterfall data or from sequential harvests. In harvests, the leaf area of several trees representative of the size-class distribution is measured. An allometric relationship is then applied to plots to estimate L^*. One commonly used relationship is that between leaf area and sapwood area. The reasoning here is that a unit or clump of foliage is supported by a number of pipes, *viz.* xylem or tracheid cells, the assemblage of pipes converging into the branches and the stem, the latter incorporating the whole conducting area from the crown base downwards. The conducting area is normally taken as sapwood area at 1.3 m (A_s, breast height). The relationship between A_l and A_s should, in principle, remain stable under a given set of conditions.

The same harvests can also be used to determine the distribution of leaf area within the canopy. This distribution is required to calculate canopy photosynthesis and canopy conductance, and to estimate transpiration.

Form of relationship and theoretical framework

In general there is a strong positive relationship, which is often linear (with slope $\Delta A_l/\Delta A_s$) between leaf area and sapwood area at breast height. Such relationships have served as useful models to predict leaf area in a range of species (e.g. conifers, Whitehead and Jarvis 1981; eucalypts, Beadle and Mummery 1990). Relationships between A_l and basal area or diameter at breast height are often as closely correlated as for sapwood area (Espinosa Bancalari et al. 1987). Closeness of fit may depend on the species investigated (Snell and Brown 1978) or stand density (Pearson et al. 1983). In *Quercus alba*, the current sapwood ring, defined as current spring growth plus the previous year's ring, was the best predictor of A_l (Rogers and Hinckley 1979).

There is a need to test the utility of leaf area/sapwood area relationships in tropical environments and with tropical species. Sapwood conducting area, the boundary between sapwood and heartwood, and variation in canopy dynamics, should be measured. It may be appropriate to sample during periods when litterfall and production of new leaf area is at a minimum. Changes in L^* during an annual cycle can then be accounted for by a calibrated indirect technique.

When estimates of L^* in fast-growing plantations before canopy closure are required, more frequent harvests may be necessary to determine the form of the relationship. Beadle and Mummery (1990) observed a large reduction in A_l/A_s in *E. nitens* during canopy development but at canopy closure the slope appeared to stabilise. The change in slope was possibly related to marked changes in partitioning from leaves to stem which occurred during this period of growth (Beadle and Inions 1990).

If transpiration rate from the average tree in the stand is assumed equal to the volume flow rate of water passing through the stem of that tree based on Darcy's law (Whitehead et al. 1984), the ratio of leaf area (A_l) to sapwood area (A_s) is given by:

$$A_l/A_S = (k_h.\Delta\psi/l).(c/D.g_S) \qquad (1)$$

where k_h is the sapwood permeability, l is the length of the stem, $\Delta\psi$ is the gradient of water potential along that length, D is the average vapour pressure deficit and g_S the mean stomatal conductance; c includes several coefficients, all of which are a weak function of temperature. The equation assumes that transpiration is from a canopy which is aerodynamically rough, an approximation for some tropical forests (Meinzer et al. 1993). Thus A_l/A_s is directly related to k_h and $\Delta\psi$ and inversely related to average D and mean g_S.

This framework was developed by Whitehead et al. (1984) to resolve an observed difference in A_l/A_s between species. In addition, application of Equation 1 is to be encouraged as a means of resolving differences in A_l/A_s between sites and in response to environment and treatment.

Sources of variation

There is a strong species dependence in A_l/A_s. Interspecific differences varied from 0.10 to 0.75 $m^2\ cm^{-2}$ in subalpine forest in Colorado (Kaufmann and Troendle 1981). This range of values for slope is of interest and both larger and smaller values of A_l/A_s are reported. Does this variation reflect real differences between species or have other factors, perhaps relating to variables in Equation 1, determined the measured slope? Whitehead et al. (1984) showed that A_l/A_s was significantly less in *Pinus contorta* than in *Picea sitchensis* (Fig. 6.5a) but that the mean k_h ($m^2 \times 10^{12}$) at breast height of the trees investigated were 4.07 and 2.05, respectively. As predicted by Equation 1, there was no significant difference in slope if A_l was related to the product of A_s and k_h (Fig. 6.5b). In Kaufmann and Troendle (1981), the intolerant species, i.e. species exposed to high radiation, had low A_l/A_s as they require higher amounts of sapwood to meet a high evaporative demand (equivalent to high D in Equation 1). Jordan and Kline (1977) reported that species in a tropical forest growing in the same environmental conditions had the same relationship between the volume of water transported and A_s.

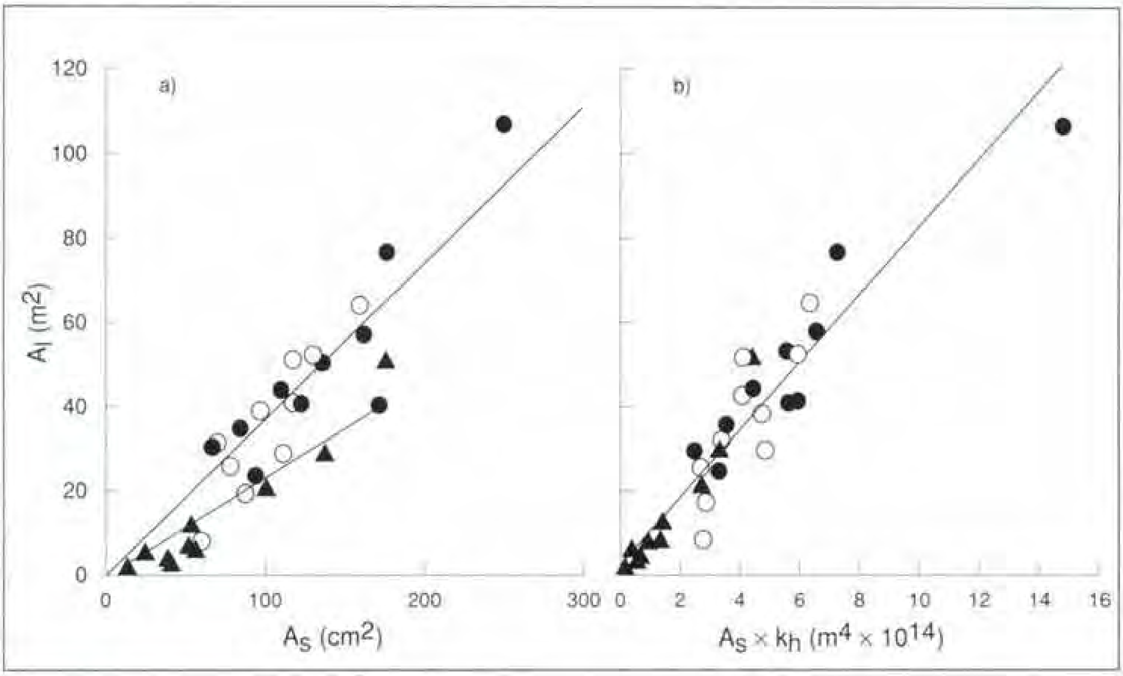

Figure 6.5 The role of sapwood permeability (k_h) in resolving differences in the ratio of leaf area/sapwood area (A_l/A_s) between species. (a) A_l as a function of A_s for *Picea sitchensis* (○, ●) and *Pinus contorta* (▲). (b) A_l as a function of A_s.k. In (a), (○, ●) are control and fertilised (with phosphorus and potassium) trees. There were no significant differences in A_l/A_s or k_h with fertilizer treatment.

The effects of site on A_l/A_s are more difficult to resolve. In some studies A_l/A_s appears stable across a range of site indices and age classes (Rogers and Hinckley 1979; Marchand 1984). In others the ratio is less predictable. A_l/A_s varied from 0.10 to 0.24 m^2cm^{-2} across five stands of *Pinus sylvestris* in Britain aged 15 to 46 yr and no clear pattern emerged (Whitehead 1978). Sites with high site index have larger trees supporting higher crown ratios and rates of transpiration than found on sites with lower indices and a positive correlation between site quality and A_l/A_s has been observed (Brix and Mitchell 1983; Binkley and Reid 1984). For 24 stands of *Abies balsamea*, there was a positive correlation between A_l/A_s and k_h. There was also a general increase in k_h with stand age which was associated with longer tracheids and larger lumen diameters (Coyea and Margolis 1992).

Equation 1 can be used to examine the impact of water stress when g_S will decrease and $\Delta\psi$ increase. These changes were quantitatively larger in *E. nitens* than *E. globulus* during drought cycles and suggested that any reduction in k_h would have been greater in the former than the latter species (White 1996). Reductions in k_h at low ψ have been observed in a range of species and are attributable to embolism in the xylem (Tyree et al. 1991). The period of recovery of k_h following a return to high levels of available water may partly determine how quickly growth rates are restored to prestress levels, and choice of species for a given site.

Any silvicultural treatment which leads to an increase in growth might be expected to increase k_h. Application of N fertilizer, with and without thinning, resulted in a significant increase in A_l/A_s compared to controls in *Pseudotsuga menziesii* (Brix and Mitchell 1983). However, there was only a small and nonsignificant increase in k_h in response to application of phosphorus and potassium fertilizers and no difference in A_l/A_s between fertilised and control plots (Fig. 6.5b). It is of interest to explore whether silvicultural options can be used to manipulate leaf area through a knowledge of the dynamics of A_l/A_s.

Indirect Methods for Measuring Leaf Area Index

Indirect methods are less time consuming than direct methods considered above and are particularly attractive for use in multi-species stands and for sequential measurements. However practice has shown that indirect methods usually require calibration against a direct method. Direct methods estimate L^* with greater accuracy because they are independent of assumptions made in the application of indirect methods.

Indirect methods are based on the optical properties of canopies. The gap fraction method relates leaf area to the probability of light passing uninterrupted through the canopy (Lang et al. 1985) by comparing the radiation environment at the base of the canopy with a simultaneous measurement above (or outside) the canopy. Their ratio measures the amount of light which is transmitted through the canopy (T). It is essential that any measurement accounts for the spatial variability of that transmittance. The basic principle is that L^* will be linearly proportional to $\ln T$.

Radiometric instruments are used to obtain the gap fraction. This can be done linearly in terms of the direct beam that penetrates the canopy (e.g. Lang and Xiang 1986) or by measurement of sunfleck area with an array of sensors (e.g. line or portable quantum sensors, Bolstad and Gower 1990), or hemispherically by measuring penetration of diffuse radiation (e.g. Chason et al. 1991). Penetration of direct beam radiation preferably requires measurement at different zenith angles whereas several are covered simultaneously with diffuse light. Fisheye photography provides an alternative approach to calculating L^* based on the entire sky hemisphere. Hemispheric methods require a field of view which is not unduly disrupted by terrain features. The volume of canopy of interest should occupy the whole field of view.

Assumptions in gap fraction methods include (i) foliage is optically black, that is any transmitted or reflected radiation measured at the base of the canopy is negligible; (ii) foliage is randomly distributed (if the foliage is clumped, leaves will tend to overlap others and will not be 'seen' by the instrument); (iii) stem and branch area make a negligible contribution to the measurement of T. Branch interception may be small where the presence of foliage effectively masks the branch area. Stem interception below the canopy is negligible. An assumption specific to measurement of diffuse beam penetration is that sky brightness is azimuthally uniform.

L^* is calculated by inversion of an appropriate radiation transfer model. One which is often used e.g. in conjunction with quantum sensors, is an inversion of the Beer's Law (see next section for definition) with L^* as the dependent variable (e.g Pierce and Running 1988). Thus:

$$L^* = -\ln(Q_F/Q_0)/k \qquad (2)$$

where Q_0 and Q_F are, respectively, the photosynthetic photon fluxes at the top of the canopy and at a point in the canopy beneath L^*. Its simplicity is based on the assumption that k adequately describes the exponential extinction of light by the canopy. k is elaborated in the text below associated with Equation 5. Values of k can be taken from the literature or obtained for the stand by measuring the attenuation of radiation through the canopy profile. As k may differ significantly between species and reported values may differ within species (Bolstad and Gower 1990), a local estimate is required but preferably from an adjacent stand so that the estimate of L^* is independent of that of k. Instruments using direct beam penetration of the canopy and hemispheric methods use more sophisticated inversion models based on gap-fraction theory. An investigation of a range of models may be beneficial to establishing a good relationship between indirect and direct estimates of L^* (Nel and Wessman 1993). The magnitude of variation in estimates of L^* for a single stand using a range of instruments and analytical models is not necessarily reconcilable by simple cross calibration (Martens et al. 1993).

A common finding is that indirect methods are well suited for examining seasonal changes in L^* and differences between treatments in relative terms. In absolute terms, they systematically underestimate L^*. Underestimates of L^* occur because foliage is grouped rather than being randomly distributed leading to a greater degree of mutual shading than is assumed by the random model. Incorporation of a grouping parameter improves the estimate of L^* but it may still be less than the direct estimate (Chason et al. 1991). However, L^* of *Quercus rubra* was similar to that obtained indirectly (Gower and Norman 1991) and estimates of L^* of a range of coniferous and broadleaf species using Equation 2 were also similar, the difference equivalent to 13% of the direct estimate and independent of canopy size (Bolstad and Gower 1990). In *Pinus caribaea* in Fiji, a similar comparison showed that indirect estimates were within 25% of those obtained from leaf biomass (Waterloo 1994). Similarly, L^* of *E. globulus* based on Equation 2 was similar to the direct estimate (Gazarini et al. 1990). L^* is usually poorly predicted by indirect methods in stands with a high L, and in stands with low L^* and a large stem and branch component, indirect methods may overestimate L^* (Deblonde et al. 1994).

To increase the utility of indirect methods and to reduce the need for calibration against direct methods, conversion factors are derived which allow for the difference between the two estimates. For example, Bidlake and Black (1989) found a linear relationship between the projected shoot area of *P. menziesii* which was seen by their fish-eye camera and the projected needle area of detached needles. The shoot or silhouette area can be measured photographically with image analysis by holding the shoot with needles attached in several positions parallel to a camera lens (Gower and Norman 1991). The ratio projected area:silhouhette area is used to define the conversion factor or grouping (clumping) index. This index has been applied to a number of coniferous stands and resulted in estimates of L^* which were not significantly different from those of the direct method (Bidlake and Black 1989; Gower and Norman, 1991).

Leaf area can be estimated by remote sensing. This is based on the marked discontinuity in the reflectance spectra of vegetation around 700 nm. As the amount of vegetation increases, red reflectance, R (600–700 nm) decreases because of absorption by chlorophyll and near-infra-red reflectance (NIR) increases because of light scattering by mesophyll tissue (Scurlock and Prince 1993). Changes in the ratio of canopy reflectance at the two wavebands is correlated with changes in L^*. The Normalised Difference Vegetation Index (NDVI) which is expressed as (R– NIR)/(R+ NIR) can replace the simple reflectance ratio.

This relationship between L^* and reflectance ratio was first established in tropical forest using transmitted light measured below the canopy (Jordan 1969). The technique is now used with aircraft-borne or satellite-mounted sensors. Good correlations between L^* and the reflectance of coniferous forest measured by an Airborne Thematic Mapper have been obtained after correction for atmospheric effects (Running et al. 1986). The spatial resolution of this technique is sufficient to measure L^* at the level of individual stands but in practice is more appropriate for investigating variation of L^* over larger areas. Good relationships have been found between NDVI and the capacity of forest canopies to intercept radiation (Waring et al. 1993).

Biomass Production and Leaf Area

Productivity can be expressed in terms of gross primary production (P_g). Net primary production (P_n) is P_g, the total amount of organic matter assimilated minus losses of that matter to respiration (R_d). Thus:

$$P_n = P_g - R_d \qquad (3)$$

P_n, the total production available to other trophic levels, including harvestable yield or stemwood yield in plantations, is expressed as the dry mass of organic matter (see Chapter 12).

Estimates of total biomass production (W) and increment (ΔW) are made from sequential harvests including partitioning into leaves, branches, stem and, in some instances, roots. The precision with which variables of yield are estimated depends on the heterogeneity of the plantation and variation between samples. What is ultimately measured as P_n requires a full understanding of the potential losses of organic matter that occur during the period of growth (t) over which yields are estimated. Thus:

$$P_n = \Delta W + L_d + L_g + L_e \qquad (4)$$

where L_d, L_g, L_e are, respectively, losses through death, to consumer organisms (herbivores and parasites), and to root exudation during t (Beadle and Long 1985).

Productivity will be overestimated if ΔW does not strictly refer to organic mass and to living material: it will be underestimated if losses occurring during t are not properly accounted for. While leaf and other litter are often collected to account for L_d, L_g and L_e are usually ignored as they are difficult to measure. In addition, few estimates of production include below-ground biomass. There may also be problems distinguishing live from senescing and dead material. These deficiencies should be appreciated in any consideration of the conversion of light energy to biomass by canopies.

An alternative approach to measuring productivity is to consider the total (gross, A_g or net, A_n) mass of carbon dioxide (CO_2) assimilated in photosynthesis. This requires continuous measurement of CO_2 flux into and out of the plantation and has the advantage of describing productivity in terms of a well-understood physiological process. Models which quantify the growth of trees initially in terms of a simple description of the conversion of light to dry mass by photosynthesis (McMurtrie and Wolf 1983; West 1987) are simply based on the impact of L^* on growth.

Light interception by canopy

Beer's Law, which describes absorption of light passing through a homogeneous medium e.g. plant pigments in solution, can be applied to forest stands. This function shows that the absorption or interception of light will be more or less exponential with increasing leaf area down through the canopy, that is, the amount of light intercepted is nonlinearly related to L^*. At any level of cumulative area F within the canopy, the rate of change of photosynthetic photon flux, Q is:

$$dQ/dF = -kQ_F \quad (5)$$

where k is a dimensionless parameter referred to as the extinction or foliar absorption coefficient. k measures the fraction of incident photons absorbed by a unit of leaf area or conversely the fraction of leaf area projected onto the horizontal from the direction of Q_0. For canopies with a *normal* distribution of foliage, most absorption of light will occur in the middle of the canopy. After integration, Q at F (Q_F) is:

$$Q_F = Q_0e^{-kF} \quad (6)$$

At the base of the canopy F is equal to L^*. Thus the level of interception is an exponential function of the product kF. If a value of 0.5 is assigned to k, it can be shown that 95% light interception occurs at $kF = 3$ which is equivalent to an L^* of 6.

In practice k is not constant and varies with solar elevation, the ratio of direct:diffuse light and any changes in canopy structure and leaf inclination and orientation which occur seasonally or in response leaf movement. A comparison between species based on measurements at maximum solar angles shows that forests have k which vary from 0.3–0.8. There appears to be little difference in the range of values of k for coniferous and broad-leaved canopies, though the largest values are for conifers. Variation within species may also be high (Bolstad and Gower 1990). Differences in k will correspond to variation in leaf angle and to degree of grouping of foliage. Canopies with leaves with low leaf angles to the horizontal have a higher k and intercept more light per unit of foliage compared to canopies with high leaf angles and lower k. k may increase if a significant proportion of light is intercepted by dead branches and stems below the canopy (Vose and Swank 1990).

For a randomly distributed canopy, k is approximately 0.5 (Monteith and Unsworth 1990). For a range of conifers, k of 0.52 used to estimate L^* was insensitive to a range of incident solar angles (Pierce and Running 1988). Application of single coefficients can be inappropriate, even for a single species, if there are large differences in stand density and canopy gaps are present (Smith et al. 1993) and L^* will be underestimated.

Photosynthesis is driven by the fraction of light intercepted by the canopy. Gross photosynthetic production (A_g) of the plantation can be expressed as:

$$A_g = A_0[1-e^{-kL^*}] \quad (7)$$

A_0 is the gross photosynthetic production at full light interception. The implication of this Equation is that there is a proportional relationship between production and intercepted (or absorbed) light and that L^* is a major determinant of the capacity of the plantation for photosynthetic production. The slope of this relationship is a measure of the conversion efficiency (ε) of light (Q, or short-wave radiation, I) to dry mass. ε has units of g MJ^{-1}. Values of ε based on Q are approximately twice those based on I. For more details on photosynthesis, see Chapter 7) and on ε, see Chapter 3).

Comparative analyses of ε for different forest types are more commonly based on aboveground dry mass (W_a) because of lack of information on belowground dry mass (W_b). ε based on W_a will be less than that based on W_a+W_b by the ratio W_a: (W_a+W_b). Partitioning of dry mass to roots may be substantially higher on a low compared to a high quality site (Chapter 8). Consequently, a comparison of ε between sites based on W_a rather than W_a+W_b would lead to a relative underestimate of the efficiency of conversion of light to dry mass on the low quality site. Similarly, partitioning coefficients for dry mass between W_a and W_b may differ between species or in species response to fertilizer treatment (Gower et al. 1997) and estimates of ε based on W_a may bear little relation to ε based on $W_a + W_b$. If significant levels of L_d, L_g and L_e (see Equation 4) occur during the period of growth considered, ε based on ΔW will inevitably underestimate ε based on P_n. This will be important in tropical environments where turnover rates are high.

The important point is that ε simply summarises the photosynthetic history of the crop over that time interval and integrates the effects of all environmental variables on the utilisation of intercepted or absorbed radiation by the photosynthetic process. The concept of ε can then be used as an important parameter for evaluating differences in growth and for predicting yield (Arkebauer et al. 1994).

Linear relationships between W_a and intercepted radiation have been observed for plantation forests. For eucalypt stands in southeast Australia ε was around 0.45 g MJ^{-1} (based on I) and independent of species and provenance within species (Fig. 6.6a). Thus differences in growth rate, in this case during the early phase of growth, can be entirely a function of more rapid development of L^* in one species compared to another. For cuttings of *Salix viminalis* and *Populus trichocarpa*, ε for production of total dry mass (W_a+W_b) was 1.58 and 1.50 g MJ^{-1} respectively (Cannell et al. 1988). These higher values illustrate that the upper limits of ε for tree species are similar to those for C_3 agricultural crops (Monteith 1977). In forests, lower values of ε are measured.

Reductions in ε occur in response to stresses of sufficient severity to reduce the quantum yield of photosynthesis. In effect the plant reduces photosynthesis by redirecting energy away from photochemistry and into photoprotective pathways which primarily disperse the absorbed energy as heat (Long and Humphries 1994). The slope will also decline as R_d becomes an increasing proportion of the carbon budget during growth.

The period of integration or time step may determine the form of the relationship between production and intercepted or absorbed radiation. In an *E. grandis* plantation, there was an apparent single linear relationship between ΔW_a and absorbed radiation on an annual time step for two treatments, one receiving irrigation and fertilizer (IF), the other a control (Fig. 6.6b). However, in a simulation study based on the spatial distribution of A_n, there was a clear separation between the treatments on a daily time step (Fig. 6.6c). The relationships remained linear, but there was a significant difference in slope between treatments, confirming that ε will be modified by factors limiting plant growth, and evidence of light saturation in the IF treatment at high levels of absorbed radiation (Leuning et al. 1991b).

Leaf area and foliar efficiency

Two relationships are often used to evaluate the impact of L^* on growth. One simply expresses dry mass production as a function of L^*, the other relates foliar efficiency to L^*. Foliar efficiency is incremental growth as a ratio of mean L^* during that period of growth. Both relationships are empirical and in many instances will be site specific. Foliar efficiency is a convenient parameter for interpreting results from comparative studies between species and treatments and for evaluating changes in efficiency with canopy size and development. Foliar efficiency includes ε and a partitioning coefficient (usually for aboveground dry mass or stem volume) but does not in itself provide any mechanistic explanation for the observed result.

The relationship between ΔW_a and L^* is linear at low values of L^* but becomes nonlinear as L^* increases (Pereira and Pereira 1989; Sheriff 1996). In *P. radiata*, for a given foliage mass, the highest levels of production were observed at a site with an abundant supply of available water and nutrients (site A, Fig. 6.7). Growth was limited by water at site B, and water and nutrients at site C, effectively reducing ε below that observed at site A. In *E. nitens*, current annual increment of stem volume increased linearly from 3 $m^3\ ha^{-1}\ yr^{-1}$ at $L^* < 2$ to > 40 $m^3\ ha^{-1}\ yr^{-1}$ at $L^* > 5$ at crown closure (Beadle and Mummery 1990). Figure 6.8 shows that foliar efficiency, expressed as the ratio of stem volume increment:leaf area, increased concurrently, and also linearly, throughout this period of growth.

In developing stands, partitioning of aboveground biomass changes rapidly from leaves to stems. In the *E. nitens* stands in Figure 6.8, partitioning of above ground dry mass to leaves changed from about 50% to <15% while that for stem wood changed from about 25% to >75%: ε remained constant (Beadle and Inions 1990). Foliar efficiency will also increase if there is a change in allocation favouring aboveground over belowground biomass (e.g. Heilman and Xie 1994).

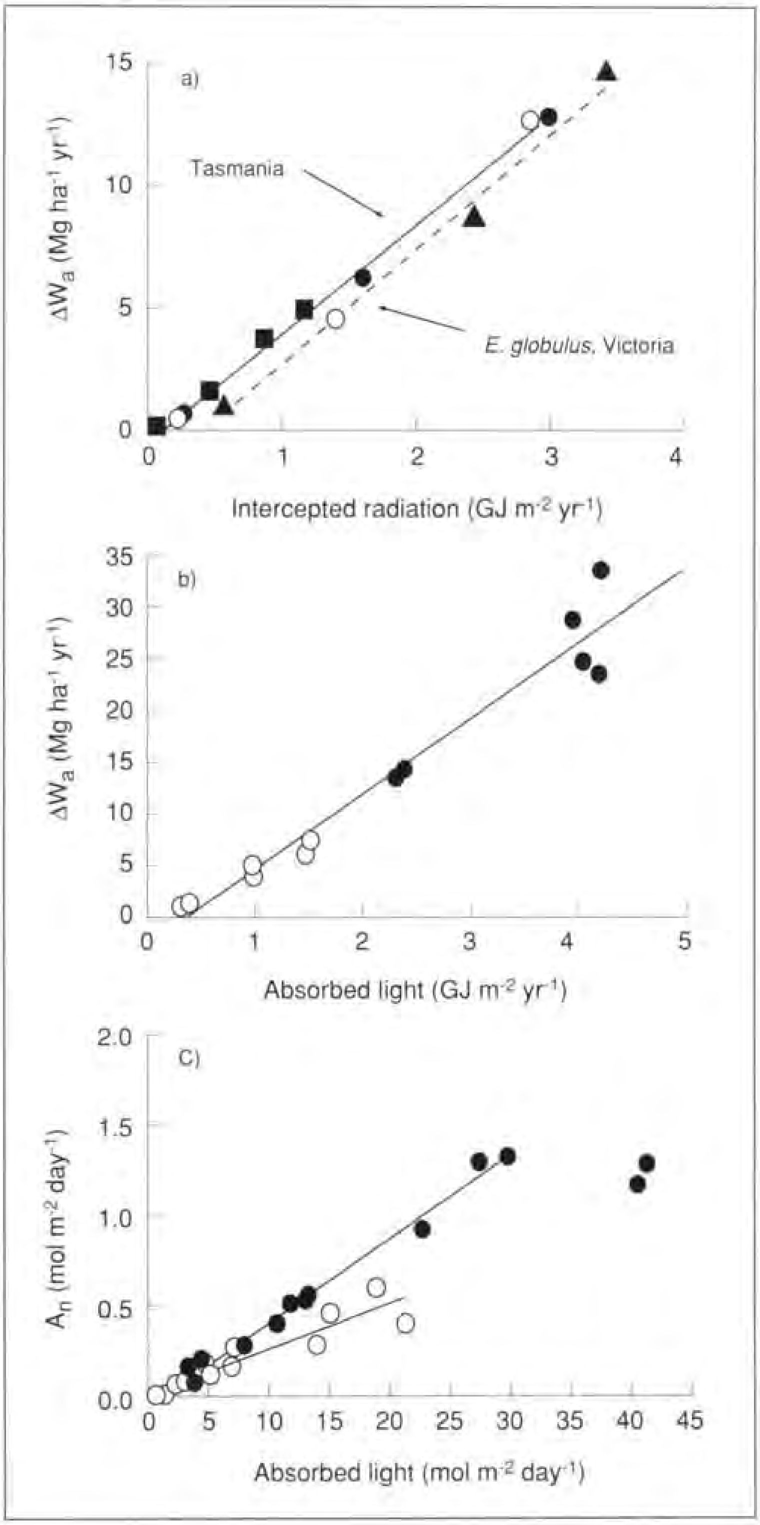

Figure 6.6 (a) Aboveground biomass production (ΔW_a) and intercepted radiation (calculated from Equation 6 assuming $k = 0.5$) in two eucalypt plantations in SE Australia, one in Victoria, the other in Tasmania. The symbols refer to three eucalypt species (*E. delegatensis*, ■ ; *E. globulus* ▲ ; *E. nitens* — two provenances, ○, ●) and pertain to the solid line (adapted from Linder 1985; Beadle and Turnbull 1992). (b) ΔW_a and absorbed light (photosynthetically active radiation) for a control (○) and irrigated and fertilised treatment (●) in a plantation of *E. grandis* in Queensland on an annual time step. (c) Net assimilation of photosynthesis (A_n) and absorbed light for the same treatments as in (b) on a daily time step (b, c adapted from Leuning et al. 1991b)

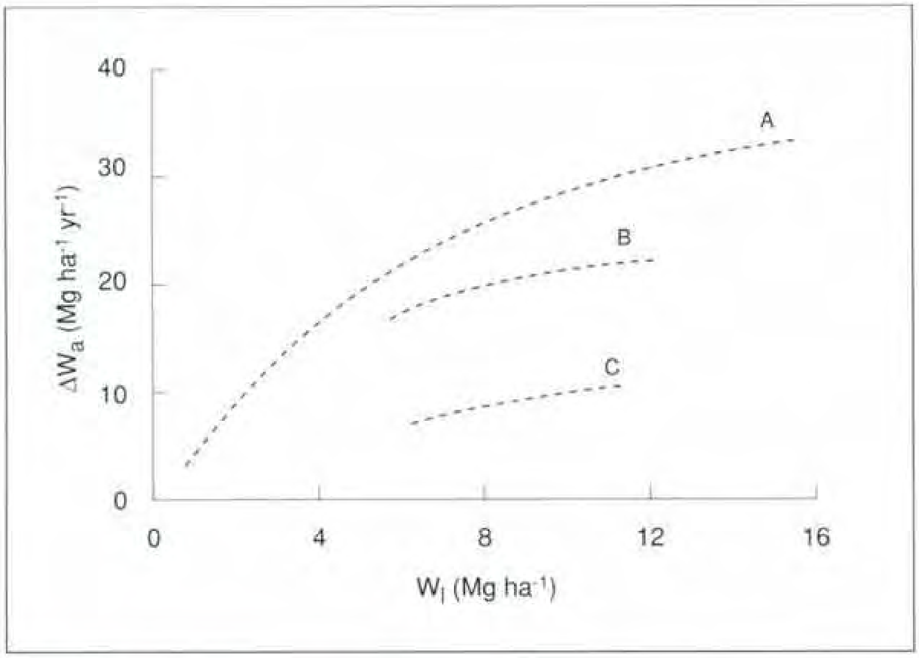

Figure 6.7 Examples of relationships between aboveground dry mass production (ΔW_a) and foliar dry mass (W_l) for three stands of *Pinus radiata*. Stand A had adequate supplies of water and nutrients for growth, stand B was limited by available water and stand C by available water and nutrients (adapted from Sheriff 1996)

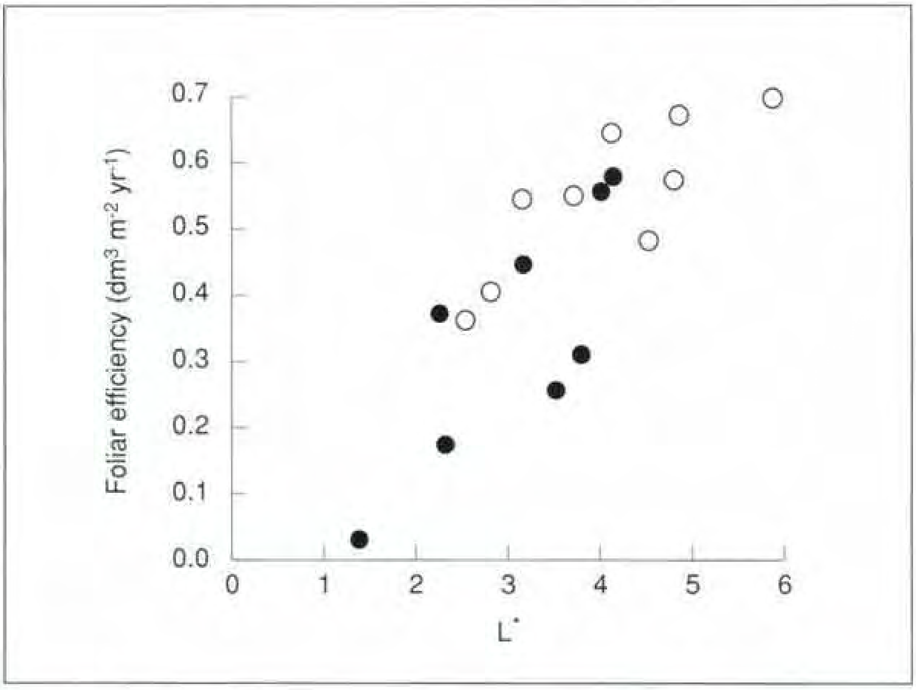

Figure 6.8 Foliar efficiency (expressed as increment in stem volume per unit leaf area (dm^{3}m^{-2}yr^{-1})) in rapidly-growing stands of two provenances (○, ●) of *Eucalyptus nitens* having a range of values for leaf area index, L* (adapted from Beadle and Mummery 1990)

As stands age, the relationship between production and L* may reach a plateau, that is L* may continue to increase with no further increase in growth rate. This may occur well before maximum L* is achieved and will be more pronounced in slower-growing stands and in species which develop high L*. Foliar efficiency of *Pinus ponderosa* decreased exponentially from >1.1 dm^3 m^{-2} yr^{-1} at very low L* to become relatively constant at $L^*>2$ (Oren et al. 1987). A decrease in foliar efficiency is inevitable if increments of aboveground biomass increase at a decreasing rate or remain constant as L* increases or if ε decreases as site resources become limiting for growth. In more open stands or in stands where thinning promotes retention and activity of the lower crown, a slower decline in foliar efficiency should be observed. An initial increase in foliar efficiency in response to thinning may occur as more light and higher levels of water and nutrients are available to the retained trees (Sheriff 1996).

Net primary production in forest stands commonly declines after canopy closure and this will be reflected as a decline in foliar efficiency. This reduction in net production is associated with an increase in the ratio of annual respiration to annual photosynthesis with increasing stand biomass (Ryan et al. 1994) and in older stands with lower rates of photosynthesis (Yoder et al. 1994). Canopy closure is also associated with the onset of intense competition between individual trees in the stand for available water and nutrients. Foliar efficiency is one means of determining the activity of the stand in relation to site resources.

A stand of 16-yr-old *Pinus caribaea* at Sao Paulo, Brazil. This stand has a high leaf area index and thus has potential for rapid growth. (Photo: E.K.S. Nambiar)

Water Use and Stand Productivity

Stand production is correlated, through transpiration, with the total quantity of water utilised by the plantation. Transpiration accounts for a considerable proportion of heat dissipation by leaves and maintains equable temperatures for photosynthetic production. Secondly, this efflux of water vapour through the stomata allows influx of CO_2 for photosynthesis. A crucial variable, with a direct link between photosynthesis and transpiration, is stomatal conductance (g_s). Stomatal conductance is a measure of the average size of the stomatal apertures. Water stress causes loss of turgor in the guard cells which in turn leads to stomatal closure and a reduction in g_s. Photosynthesis declines and, at a given level of atmospheric deficit (evaporative demand), there will be a proportional reduction in transpiration (see Chapter 7).

The availability of stored water for the growth of forests will largely depend on inputs of water through rainfall and properties of the soil profile which determine its water holding capacity. Water can also be extracted from reserves at depth. This is not a sustainable source though could be essential for tree survival in a protracted dry season. Transpiration (E_t) is a function of the available water, the evaporative demand, the stomatal control of water loss and the extent of the evaporating surface measured as L^*. Water can also be evaporated from wet surfaces during and following rainfall. This loss of water back into the atmosphere is referred to as rainfall interception (E_i). Water lost by interception is not available for growth. Canopy structure and area contribute to this process and it is clearly of benefit to understand the potential consequences on production of water foregone to interception. For a detailed consideration in rainfall interception, see Chapter 5).

Transpiration

Several approaches are used to estimate transpiration by forest stands. Transpiration estimated from physiological measurements in the canopy is the only method which requires explicit use of L^*. Stomatal conductance (g_s) is measured by sampling throughout the canopy and canopy conductance (g_c) determined as the product of g_s and L^*. For plantations with low L^*, the canopy can be considered as a single leaf but for large canopies, an appropriate multi-layer model is used (Roberts et al. 1992). Thus:

$$g_c = \Sigma L^*_i . g_{s,i} \qquad (8)$$

where i is the ith horizontal layer in the canopy. g_c is then incorporated into the Penman-Monteith equation (see Chapter 3) to estimate E_t. From Equation 8 this takes the form:

$$\Sigma \lambda E_{t,i} = \Delta . R_{n,i} + \rho . c_p . \delta q, i . g_{a,i} / (\Delta + (c_p/\lambda) . (1 + g_{a,i}/g_{c,i}) \qquad (9)$$

where $R_{n,i}$ is the net radiation absorbed by the canopy and $g_{a,i}$ the boundary layer conductance in layer i. $\delta q,i$ is the canopy layer specific humidity deficit and λ, ρ, Δ, c_p, constants, respectively the latent heat of vaporisation of water, the density of air, the rate of change of specific humidity with temperature and the specific heat of air.

Roberts et al. (1992) applied Equations 8 and 9 to young plantations of *Eucalyptus camaldulensis* and *E. tereticornis* in southern India (Fig. 6.9). Although L^* was increasing in 1988, E_t declined from a maximum of about 3–4 mm day^{-1} during the monsoon as the evaporative demand (δq) was low. At the beginning of the dry season, E_t rose sharply with an increase in δq but then declined, primarily in response to stomatal closure, as levels of available moisture became severely depleted. This pattern was repeated in the following year though maximum rates of E_t had increased to 6 mm day^{-1} due to a further increase in L^* (Fig. 6.9). In subtropical South Africa, E_t of *E. grandis* with L^* of 4.2 varied from a minimum of 2.4 mm day^{-1} to a maximum of 8.9 mm day^{-1} during periods of high δq (Dye 1987). If stand production is proportional to water use, maximum rates of growth will be maintained as long as E_t can meet the evaporative demand. As low levels of available water persist for significant periods in many tropical climates (see Fig. 5.1) growth will not be sustained at potential rates. Selection of species, particularly evergreen species, for tropical plantations should include a consideration of their drought tolerance characteristics and their ability to maintain low rates of E_t during protracted periods of low available moisture and high evaporative demand.

The differing ability of species to quickly build up leaf area is illustrated in this photograph of four-yr-old, closed canopy stands of *Eucalyptus delegatensis* (L) and *E. nitens* (R) at Esperance, Tasmania. The L*s are 2.2 to 2.4 respectively. (Photo: C.L. Beadle)

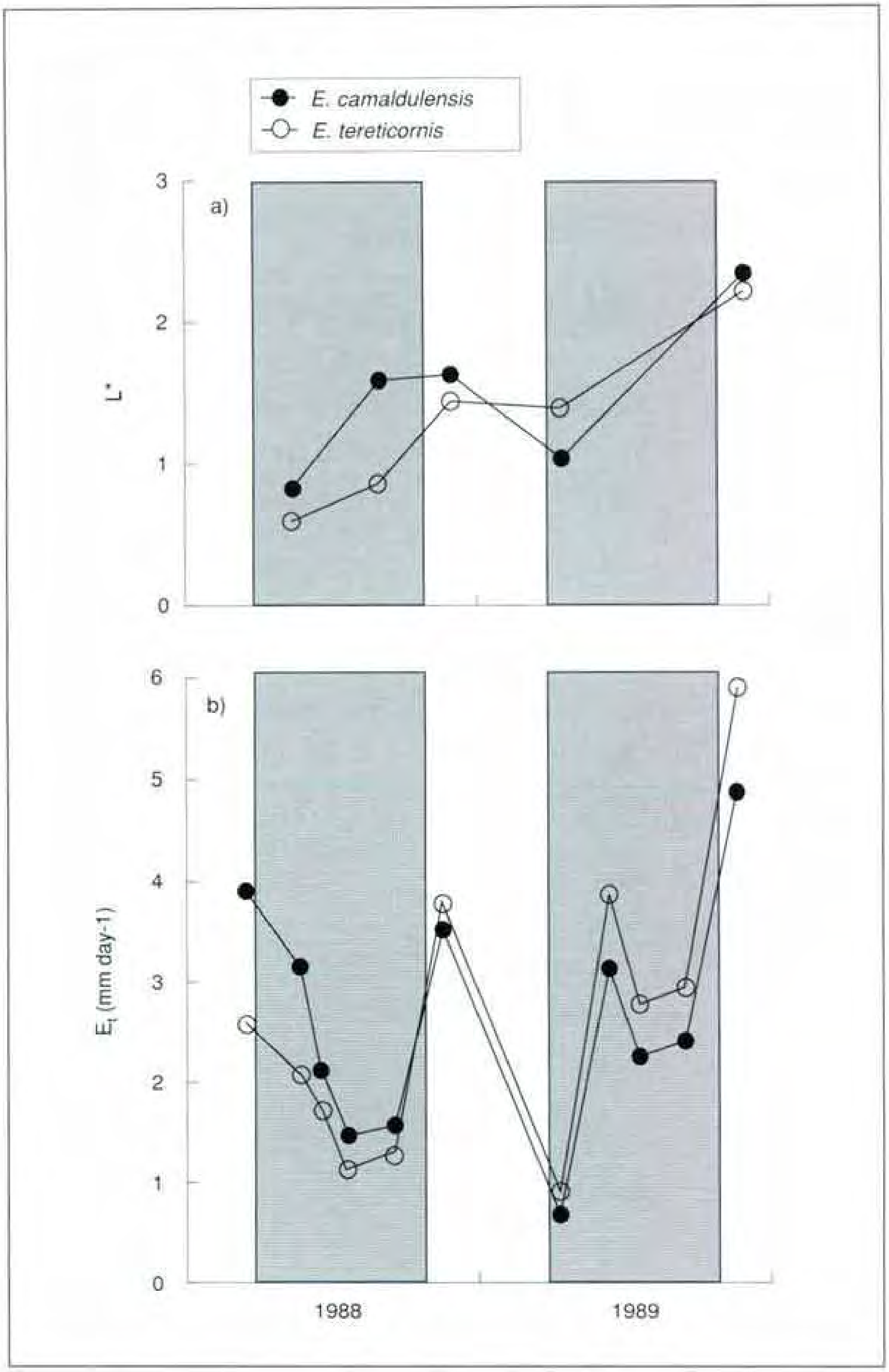

Figure 6.9 Daily transpiration (E_t) and leaf area index (L*) of *Eucalyptus camaldulensis* and *Eucalyptus tereticornis* over two seasons at a site in southern India. The shaded areas are the monsoonal periods and the clear areas the dry season (adapted from Roberts et al. 1992).

A useful measure of total water use during an annual cycle is the crop factor. The crop factor expresses transpiration as the ratio of total pan evaporation (E_0) for the same period of growth (i.e. E_t / E_0). On sites where available water is not limiting growth and canopy development, Figure 6.10 shows that crop factor increases with the size of the canopy and, for a range of eucalypt species and *Pinus radiata*, crop factor was 0.9 at canopy closure. Where available water limits growth and canopy size, the maximum crop factor is lower. For example, the crop factor of *E. camaldulensis* and *E. tereticornis* was about 0.6 at three sites in southern India, total water use by the canopies being approximately in balance with rainfall (Harding et al. 1992). Effectively, L^* acts as a critical integrator of levels of available water (Gholz et al. 1990). Mean annual rainfall is often a useful indicator of available moisture and the potential for growth.

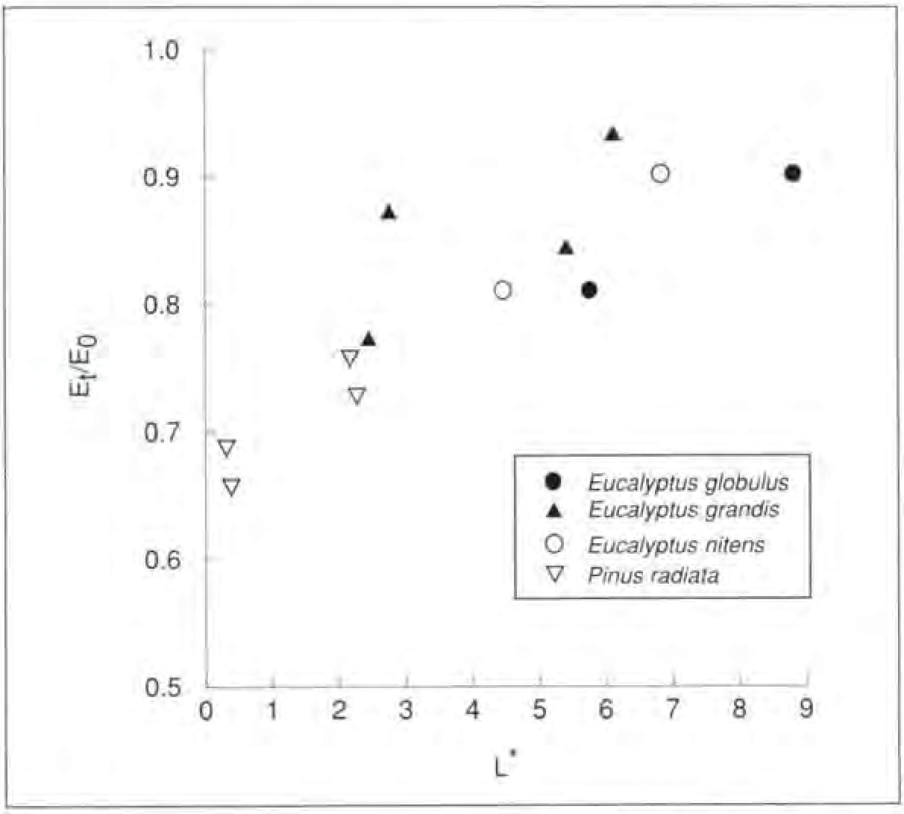

Figure 6.10 The annual crop factor (expressed as the ratio of actual transpiration (E_t) to potential evaporation (E_0)) as a function of annual mean leaf area index (L^*). The sites were in New South Wales, Australia and Tasmania, Australia and were, respectively, effluent irrigated (*Eucalyptus grandis, Pinus radiata*) or irrigated (*E. globulus, E. nitens*) so that available water did not limit growth. (Adapted from Myers et al. 1996; Honeysett et al. 1996 and White 1996. E_t for the Tasmanian data was calculated assuming that E_i=0.15E (where $E=E_t+E_i$))

Changes in E_t and L^* are not proportional (see Fig. 6.10). This occurs because changes in L^* also affect the microclimate in the canopy and the distribution of δq and g_S. In general small canopies are more exposed and in relative terms δq will be higher than for large canopies though this difference will decrease as the aerodynamic roughness of the canopy increases. g_s may also be higher throughout a greater proportion of smaller canopies as there is less self shading than in larger canopies. The overall effect is that increases in E_t with L^* will be higher at low than at high L^*. In a comparative analysis between *E. nitens* and *E. delegatensis* over two growing seasons, Honeysett et al. (1992) observed that a twofold difference in L^* and stem volume increment was associated with differences in evapotranspiration ($E=E_t+E_i$) between species of less than ten per cent. In a similar analysis over a wider range of species and sites Roberts (1983) showed that there was very little variability in E_t and argued that negative feedback of δq, which results in stomatal closure, tends to equalise E_t between forests. In *E. grandis* plantations adequately supplied with water and nutrients, this response was sufficiently sensitive to cause a negative relationship between standing stem volume at age three yr and mean annual E_0 (Myers et al. 1996). This result suggests that plantations established on sites with high evaporative demand will grow at lower growth rates, even in the absence of water stress, than on sites where the evaporative demand is lower.

Changes in the water-use characteristics of forests in response to increasing L^* have been investigated in terms of concurrent changes in maximum values of canopy conductance, $g_{c,max}$, and surface conductance $g_{S,max}$ using appropriate forms of the Penman-Monteith Equation (Fig. 6.11, Schulze et al. 1994). Surface conductance accounts for the combined transfers of water vapour from the soil and the canopy. The model demonstrates that $g_{c,max}$ increases linearly at low values of L^*. At $L^* > 4 < 6$ the relationship is strongly curvilinear and at $L^* > 6$, $g_{c,max}$ remains constant and converges with corresponding values for $g_{S,max}$ as soil evaporation under large canopies is negligible. As L^* decreases below 6, soil evaporation becomes an increasing component of total evapotranspiration from the canopy in response to greater penetration of available energy through the canopy. The implication of this analysis is that soil evaporation can form a significant proportion of E from dry canopies when L^* is < 4 but that its contribution rapidly becomes negligible for larger canopies (Myers and Talsma 1992). Wet soil conditions and two levels of mean $g_{s,max}$, 12 and 4 mm s^{-1}, were assumed in this analysis. These boundaries incorporated measured values of $g_{S,max}$ from all forest types including those from tropical environments (Fig. 6.11). As the soil dries, its contribution to evapotranspiration will decrease. If levels of available water decline to levels which cause stomatal closure, g_c and E_t will also decrease.

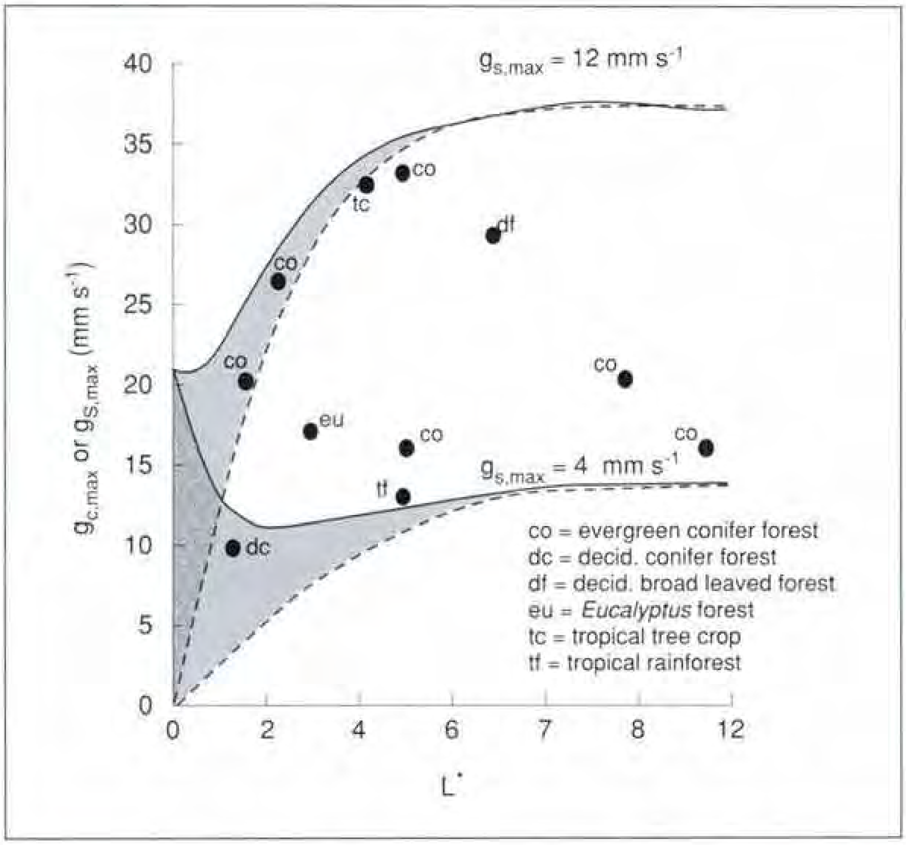

Figure 6.11 The relationship between maximum surface ($g_{S,max}$, solid line) or canopy ($g_{c,max}$, broken line) conductance and leaf area index (L*). The lines represent modelled values determined from an appropriate Penman-Monteith equation for two values of maximum stomatal conductance ($g_{s,max}$) and the points measured values from a range of forest types. The shaded area measures the difference between $g_{S,max}$ and $g_{c,max}$ and represents the contribution from soil evaporation. Note that there is little change in conductance and therefore E_t at L*>6 (adapted from Schulze et al. 1994)

Rainfall interception and canopy storage of water

Bruijnzeel (Chapter 5) has considered fluxes of water including rainfall interception in relation to hydrological balance and land use. For managers concerned with plantation establishment and productivity, the issue of interest is the role of rainfall interception as a determinant of available water. Thus evaporation of intercepted rainfall is potentially water foregone for growth and wood yield.

Conversely, interception of fog and mist by canopies may result in a net gain of water into forests (Costin and Wimbush 1961).

The evaporation of intercepted rainfall (E_i, hereafter called interception loss) is a function of micrometeorological variables and the water-holding capacity of the canopy. Interception loss is also related to transpiration in the sense that energy is required to drive both processes and diversion of energy into E_i reduces that available for E_t. Interception loss is almost entirely driven by atmospheric deficit and primarily a function of the aerodynamic roughness of the canopy and windspeed (Kelliher et al. 1992).

Interception loss includes evaporation of water stored on the surface of tree canopies and evaporation while the rainfall or storm event is in progress. The amount stored by the canopy when rainfall and throughfall (the component of rainfall which is not intercepted) have ceased is referred to as the canopy storage capacity (S). Water can also be stored on branches and stems and this is referred to as the trunk storage capacity (S_t). If the trees have thick fibrous bark, S_t can be a larger contributor to E_i than S (Crockford and Richardson 1990a).

Teklehaimanot and Jarvis (1991) demonstrated that storage capacity was a property of individual trees and that there was a linear relationship between S and the number of trees in the stand and, by inference, S and L^*. While S is a function of L^*, the retention of rainfall depends on leaf shape and their surface characteristics: raindrop size, momentum and windspeed also impinge on retention (Jackson 1975). Canopy capacities are therefore found to vary with environment and species. Both S and S_t may also vary with the disposition of the leaves and branches (Blake 1975) and the size of the storm (Lloyd et al. 1988).

Estimates of S and S_t for tropical plantations are few and consistent patterns have not emerged. For *Acacia auriculiformis*, S and S_t varied between 0.5–0.6 and 0.037–0.087 mm, respectively, in a 4- to 5-yr-old stand (Bruijnzeel and Wiersum 1987). Waterloo (1994) reported that S was 0.8–1.4 mm across stands of *Pinus caribaea* in Fiji: this was reduced to 0.3–0.6 mm following a cyclone and reduction in L^*. Systematic differences between eucalypts and pines appear well established, suggesting a larger S in the latter (e.g. Calder 1986). A higher S for pines than eucalypts is also used to support the observation that E_i is proportionately larger in pines (Crockford and Richardson 1990b). However these differences may be related to low L^* of the eucalypt stands investigated, as well as to structural attributes which affect evaporation rates (Dunin and Mackay 1982). Where canopy structure has received attention, the presence of smooth rather than rough bark and differences in leaf orientation and morphology, leading to less residence time of water in the canopy, are attributed to the lower E_i of eucalypts than pines (Feller 1981; Poore and Fries 1985).

Synthesis

Several environmental factors determine the growth of trees through their effects on physiological processes. These effects can be summarised in terms of the amount of light which is captured by canopies and converted into dry mass. Canopy size is a key variable determining energy capture and this chapter has shown that the relationship between dry mass production and light interception provides a useful framework for determining the impact of L^* on the productivity of tropical plantations.

Plantations are established on sites which are initially free of vegetation. Rapid site occupancy by the plantation species is desirable to minimise the potential impact of competition for site resources. One of the benefits of using *Eucalyptus* and *Acacia* species in tropical plantations is that their high early growth rates minimise the time taken to reach maximum canopy size. With a few exceptions, less is known about rates of development of coniferous and deciduous species in the tropics and this knowledge would assist in the development of appropriate silvicultural practices for managing vegetation during plantation establishment.

The demand for water and nutrients increases during canopy development and it is clear that the level of supply at a given site will determine canopy size. Several experiments, often incorporating irrigation and nutrient addition, have shown that the rate of canopy development and ultimately canopy size can increase under intensive management but this result has not necessarily added to an improved understanding of the interactive effects of water and nutrients on canopy size or of the key processes which sustain canopies throughout a rotation. A thorough evaluation of these issues is crucial to the success of plantations in tropical environments where site disturbance during clearing and inter-rotational management practices may have negative impacts on inherent site quality and productivity in the longer term. Regular monitoring of L^* is a valuable means of measuring these impacts and will act as a useful indicator of changes in site quality and productivity and of any requirement for ameliorative treatments, such as later-age fertilisation, during the rotation. New experiments should incorporate other measures of site quality such as soil organic matter and soil physical properties, as well as a determination of the level of available water and nutrient supply, to assist in the interpretation of observations. The methods outlined in this chapter for measuring L^* are now well established. The potential for large changes in leaf area over short periods in the tropics calls for the incorporation of indirect methods if the technologies supporting this approach are affordable. Calibration of instruments against destructive harvests is essential and these harvests should be of sufficient frequency to check for any changes in the relationship between leaf area and conducting area.

Periodic cycles of water stress will impinge on the productivity and ultimate success of plantations in many tropical environments. An assessment of rates of leaf expansion and the life span of leaves is relatively simple. The water stress integral should be used as a means of evaluating the cumulative effects of stress, if possible, as this provides a firm foundation for comparing the degree of tolerance to stress that a species displays in a particular environment. Selection of a species for plantations ultimately depends on its ability to survive, but we must look for characteristics in a species which combine drought tolerance with efficient use of available water. This may require species which shed foliage with increasing water stress but which are also capable of rapid canopy development when an adequate level of available water is restored. A knowledge of the water use characteristics of a species and how this is related to canopy size and leaf dynamics will also assist the correct choice of species for a site.

Acknowledgments

This chapter was written while on study leave in the U.K. and I am grateful to John Roberts for allowing me access to his literature base. I also thank Maria Cherry for assistance in preparation of the manuscript and figures.

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7

The Ecophysiological Basis for Productivity in the Tropics

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Abstract

In this review we establish a conceptual framework for the interpretation of physiological data in the context of understanding the environmental controls over productivity of tropical tree plantations. We conclude that available data specific to tropical trees are generally scarce, with most information available only for the two currently-dominant genera of *Pinus* and *Eucalyptus*. With respect to these two genera, it is clear that the available knowledge of their ecophysiological responses, both in their native habitats and exotic environments, has provided a valuable scientific basis for their management in plantations. There is little published information concerning most native species, some of which may have high potential for plantation use.

There are also significant limitations on the usefulness of physiological data and physiologically-based models for addressing day-to-day forest management issues. These include: 1) a lack of understanding of how the partitioning of carbon, fixed during photosynthesis, among various tree tissues is controlled, which limits most models to the canopy level; and 2) the inability in any case to validate simulations based on physiological processes at the stand level, which may be addressable given recent advances in the independent measurement of whole-forest fluxes of CO_2 and water.

Although some major issues, such as the relative use of water by highly productive trees and stands of *Eucalyptus* in comparison with other tree species and competing land uses, are ultimately resolvable, the debates will continue. Significant progress in the development and application of models to the reliable prediction of productivity will most likely result when physiological, environmental and stand gas flux data are collected as integral parts of studies addressing the growth of tropical tree plantations. Such advances would also help to resolve conflicting views about the impact of plantation forestry on other land use values (e.g. available water) and to improve options for managing productivity. In most cases, methodology for studying physiological processes at various levels — from tissue to ecosystem — in the tropics can be readily adapted from what has been achieved by research on temperate forest systems.

PRODUCTIVITY OF tropical tree plantations varies appreciably. Numerous factors contribute to this. Successful plantation development has occurred when there has been detailed background information about the species and environmental conditions of the plantation site, and when such information has been used in developing effective management strategies. Many failures can be attributed to an inappropriate match between the characteristics of the selected species and the above and belowground environments into which trees have been introduced. An understanding of the ecophysiological basis of productivity, and how various environmental factors interact with the physiology of the species, is important for the continued development and successful management of plantations.

In this chapter we explore the critical linkages between physical and chemical environmental conditions and the physiological processes that collectively determine annual carbon accumulation rates for trees in tropical environments. In addition, we discuss how these processes can be combined into models of tree growth and primary production at spatial scales from the leaf to stand. The level of physiological detail necessary for inclusion in such models varies greatly. For example, it may not be necessary to incorporate leaf biochemical reactions into models of stand development over a period of years to decades. However, an understanding of the physiological underpinnings (or assumptions) of any productivity model is essential for proper application and interpretation of the results. This is particularly true for tropical tree plantations, where actual data on which to base productivity predictions may be sparse, with a high degree of reliance on information from different tree species growing in non-tropical conditions.

In fact, it is not possible to construct an exhaustive review solely based on tropical species planted in their natural environments. This is because the possible combinations of species, soil and environmental characteristics are virtually limitless, while the most extensively planted and well-studied genera in tropical environments are two that in most cases are exotics, *Pinus* and *Eucalyptus*. Fortunately, these two genera are highly contrasting in their ecophysiological characteristics, so that they should still serve as useful as comparative examples for discussion. Whenever possible, we will also incorporate the less-complete information on some other important plantation tree species and use results from more temperate environments as necessary to make particular points.

A Conceptual Model for Carbon Gain

A simple equation can represent the instantaneous net carbon gain for an individual tree:

$$C_n = A_c \times L - E\,(R_t \times B_t) \qquad (1)$$

where A_c is the mean canopy-level value of net photosynthesis per unit of leaf area (A), L is the canopy leaf surface area, R is the specific respiration rate of the non-foliar tree tissues, t (e.g. branches, stems, roots), and B is the biomass (or equivalent area) of the tissues. The product of R_t and B_t is summed over the entire tree.

The accumulation of L on any specific site (for a whole stand this becomes the leaf area index, or L^*) and the relative distributions of tissue biomass are controlled by both physical and chemical factors of the environment and are discussed elsewhere in this volume. Most research on the remaining terms has focused on photosynthesis and respiration of leaves, although there have been small surges in reports on respiration of other tissues. It is also possible to reformat Equation 1 by separately considering gross photosynthesis and foliar respiration, although most measurements are made using small chambers and, thus, measure net CO_2 exchange (gross photosynthesis less respiration).

In theory, the sum of instantaneous net carbon gain of all the trees, over a year and at the level of the stand, is net primary production (NPP) (see Chapter 12). In practice, the relationship between instantaneous carbon gain and NPP is more difficult to establish, as plant parts—continuously or periodically—are created, grown and shed. A key additional difficulty (discussed below) for the prediction of stem growth is in determining the controls over assimilate partitioning between roots and shoots.

Finally, although there may be less seasonality to temperatures in the tropics than in higher latitudes (see Chapter 3), many tropical ecosystems are characterised by extremes in water availability and the dynamics of nutrient availability are only poorly understood for most combinations of tropical soil and tree (Silver 1994). Therefore, extrapolations based on short-term, small-scale physiological measurements—the norm for studies in remote areas such as much of the tropics—to the stand level are unfortunately likely to be no more reliable than those made for higher latitude forests.

Controls Over Photosynthesis

Photosynthesis is affected by many environmental factors, but primarily by incident radiant energy, temperature, water and nutrient availability. In addition, there is some circumstantial evidence that forests are already responding to global increases in atmospheric carbon dioxide concentrations, although this is highly controversial. Atmospheric inputs of nitrogen (N) have also increased significantly in many tropical regions, particularly in areas influenced by large amounts of biomass burning or agricultural fertilisation (Clark 1994), as no doubt have localised air concentrations of ozone and other potentially harmful chemicals near pollution sources (e.g. near urban areas in closed valleys or downwind from particular point sources).

Although environmental factors interact and are often highly correlated (e.g. diurnal patterns of air temperature and incident radiation flux), we will first briefly treat each one in isolation.

Radiant energy

High incident radiation imposes a direct energetic challenge to tree leaves which may either: 1) avoid absorption; or 2) absorb and pay the costs of dissipation in terms of water use; or 3) absorb and pay the costs of tissue heating above ambient temperatures.

Maintaining leaves significantly above ambient temperatures can cause excessive respiratory carbon losses, if not tissue damage, and is not, therefore, evolutionarily advantageous. However, it has been observed in Florida (Syvertsen and Albrigo 1980) that sun-exposed leaves of citrus (an intensively managed exotic broadleaf species in that setting) often exist at internal leaf temperatures in the summer up to 10°C higher than ambient, cooled only through the evaporation of irrigation water off their surfaces. In this case, irrigation at the soil surface may meet demands for water at the root surface, but not be sufficient to maintain a positive leaf carbon balance and, hence, the expected high plant productivity and fruit yields.

Small leaves (e.g. conifer needles, highly dissected palm fronds, the leaflets of many leguminous trees) have high boundary layer conductances—usually much larger than corresponding stomatal conductances—and will normally dissipate enough absorbed energy through convection and transpiration to exist at or near ambient temperatures under virtually all conditions (Gates 1980). However, very large leaves may have stomatal conductances that in fact exceed boundary layer conductances. There are many other mechanisms for reducing radiation absorption (e.g. vertical leaf display, more reflective surface coatings) that are well-documented in the literature; their relative contributions can be evaluated using straightforward models (Schuepp 1993).

The shape of the photosynthesis-radiant energy response curve for a wide variety of trees, at given levels of the other essential environmental resources, is well-established (e.g. Fig. 7.1). However, even though the flux of incident radiation in the tropics is high, much of the canopy exists at considerably lower light levels due to the negatively exponential relationship between light penetration and accumulated leaf area as you move down through the canopy, especially in stands with already high total L^*. This means that the initial slope of the response curve at low light levels (often referred to as apparent quantum yield) may be more important than the light-saturated value of photosynthesis in controlling carbon gain of closed canopy stands. Consequently, the relationship between photosynthesis integrated over an entire tree canopy and intercepted light becomes more linear (Fig. 7.1). Data of this latter sort are generally obtainable only through extrapolation of large numbers of leaf-level measurements (e.g. Beadle et al. 1985), through modelling (e.g. McMurtrie and Wang 1993) or using micrometeorological techniques such as eddy correlation (e.g. Leuning and Moncrieff 1990; Wofsy et al. 1993) (see Scaling below in 'Integrating Environment and Ecophysiology').

The values of the apparent quantum yield reported in the literature for five tropical broadleaf tree species (Table 7.1) range from around 0.045 for two species of *Eucalyptus* to over 0.1 for *Hevea*. Although it is hard to make a case with so few points, this contrasts with the range presented for pine species, for which the maximum reported value is 0.03. *Pinus elliottii*, a humid-subtropical pine species, has the minimum value reported for the pines. There is a good theoretical basis on which to conclude that quantum yields under ambient CO_2 conditions cannot exceed about 0.05. Reported higher values are likely to be due either to experimental error or to measurements made at low light levels where dark respiration is turned off by increasing light levels (the Kok effect) (Kirschbaum and Farquhar 1987). What would be more experimentally useful would be studies of how close leaves might get to a theoretical maximum value and the factors which cause them to fall below that value. Values of maximum photosynthesis per unit of leaf area range from around 3 to 27 mmol m^{-2} s^{-1}, with pines again at the lowest end of the range. Various species of *Eucalyptus* are represented at both the minimum and maximum among non-pine species. Part of the variation may be due to methodological differences among the studies, particularly the way in which leaf area is expressed (e.g. on a total vs projected area basis; Chapter 6). However, the large apparent range both within and among species suggests one reason for the highly variable growth responses observed for stands of different species to silvicultural manipulation that affects the light environment of tree crowns.

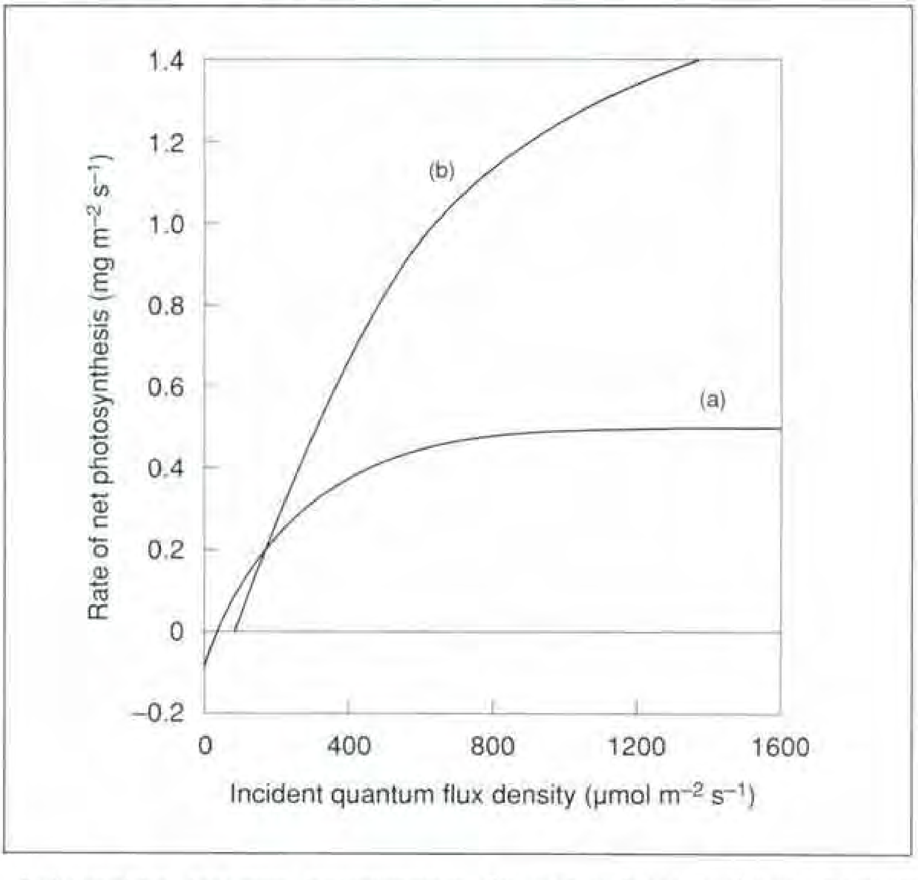

Figure 7.1 Relationships between instantaneous Pn and incident radiation (PAR) for *Picea stichensis*: (a) needles and (b) whole canopy (from Jarvis and Leverenz 1983)

Table 7.1 Comparative rates of light-saturated photosynthesis (A_0), apparent quantum yield (α) and maximum stomatal conductance ($g_{s,max}$) for tropical tree species. Data are from plants grown at ambient (or 350 ppm) CO_2 and are maxima (if a range was provided) unless noted.

Species	A_0 (mmol m^{-2} s^{-1})	α	$g_{s,max}$ (mmol m^{-2} s^{-1})	Reference
Acacia melanoxylon	8.5			Küppers et al. 1986
Albizia antunesiana	11.9 ± 2.7			Tuohy et al. 1991
Bischofia javanica	10.6 ± 0.3	0.063		Kamaluddin and Grace 1993
Cecropia spp.	17.5		500[a]	Reekie and Wayne 1992
Erythrina variegata	6.2 ± 0.06		235	Muthuchelian et al. 1989
Eucalyptus behriana	14.0			Küppers et al. 1986
E. blakelyi	6.0			Mooney et al. 1978
E. camaldulensis	12, 26[b]		400, 470	Lima et al. 1995
E. camaldulensis	16.2		625	Ferrar et al. 1989[c]
E. camaldulensis	11.5		223	Luangjane 1990
E. camaldulensis			700	Roberts and Rosier 1993
E. delegatensis	17.0			Küppers et al. 1986
E. globulus	7.0		245	Pereira et al. 1987
E. gracilis	11.4			Mooney et al. 1978
E. grandis	23.1[d]			Kirshbaum and Tompkins 1990
E. grandis	8.5			Mulligan 1989
E. grandis	11, 25[b]		450, 310	Lima et al. unpublished data
E. gummifera	11.5			Mulligan 1989
E. incrassata	25.5		1200	Ferrar et al. 1989[c]
E. maculata[e]	21.0			Wong and Dunin 1987
E. maculata/Acacia[e]	27.0	0.049	100	Wong and Dunin 1987
E. melliodora	6.7			Mooney et al. 1978

Table 7.1 (cont'd) Comparative rates of light-saturated photosynthesis (A_0), apparent quantum yield (α) and maximum stomatal conductance ($g_{s,max}$) for tropical tree species. Data are from plants grown at ambient (or 350 ppm) CO_2 and are maxima (if a range was provided) unless noted.

Species	A_0 (mmol m^{-2} s^{-1})	α	$g_{s,max}$ (mmol m^{-2} s^{-1})	Reference
E. miniata	11.6		400	Ferrar et al. 1989[c]
E. pauciflora	16.3		650	Ferrar et al. 1989[c]
E. pauciflora	26.0	0.042		Küppers et al. 1986
E. phaeotrica	13, 30[b]		610, 500	Lima et al. 1995
E. pilularis	5.8			Mooney et al. 1978
E. pilularis	8.0			Mulligan 1989
E. saligna	3.7			Mooney et al. 1978
E. socialis	7.5			Mooney et al. 1978
E. tereticornis			500	Roberts and Rosier 1993
E. torelliana	13,26[b]		400, 350	Lima et al. unpublished data
E. urophylla	11,22		400, 20	Lima et al. unpublished data
Gmelina spp.			670	Whitehead et al. 1981
Gmelina spp.			535	Osonubi et al. 1985
Hevea brasiliensis	22.2	0.114		Ceulemans et al. 1984
H. pauciflora	14.1	0.102		Ceulemans et al. 1984
Pinus elliottii	3.2	0.005	40	Teskey et al. 1994a
Pinus spp. (range)	2.0–6.7	0.005–0.031	30–180	Teskey et al. 1994b
Tectona spp.			1340	Whitehead et al. 1981
Theobroma cacao			558	Valle et al. 1987

[a]Assuming value of 0.5 in the reference was missing 10^3 in units; [b]Values for seedlings grown in 350 or 700 ppm CO_2, respectively; [c]For seedlings grown under 'high temperature' conditions; [d]Grown hydroponically with high P in the mist solution; [e]For a mixed natural stand enclosed in a chamber

Water

There is a strong interaction between water and temperature (next section) conditions of the ambient air. The generally high air temperatures in lowland tropical environments create a high degree of sensitivity to small variations in relative humidity in determining air saturation deficits. For example, a 10% decrease in the relative humidity at 40°C results in 2.5 times the air saturation deficit as an identical decrease at 20°C (Campbell 1977). This means that species whose stomata are sensitive to air saturation deficits may experience significant periods of reduced photosynthesis even with relatively abundant soil water supplies. As temperatures moderate with elevation, montane forests are generally both cooler and more humid.

Soil water deficits and or high saturation vapour deficits of the air may impose the most widespread limitations on plantation carbon gain and NPP in the tropics, given the generally high radiation fluxes and temperatures. Even in the most humid regions, large forest clearings (e.g. abandoned pastures) may experience greatly elevated temperatures and lowered relative humidities at the ground surface, creating an inhospitable environment and prohibiting the planting of any but the most hardy tree species. Water deficits can lead to many, often simultaneous, plant responses (Kramer 1983).

L_* can adjust to match site water availability (cf. Grier and Running 1977); completely drought-deciduous trees, such as *Ceiba pentandra*, *Erythrina*, *Cordia alliodora* and *Tabebuia neochrysantha*, take such 'drought avoidance' to an extreme. However, warmer temperatures may also lead to lower L_* if internal carbon availability is insufficient for maintenance (Cropper and Gholz 1994, see Temperature below).

Carbon gain may be sacrificed as L_* is reduced in response to a water deficit, although this will depend on the initial level of L_*, on the degree of reduction of L_* and on other aspects of stand and canopy geometry that influence the pattern of radiation distribution within individual crowns (Stenberg et al. 1994; Nilson and Ross 1997; Chapter 6).

Stomatal conductance may also be affected, either directly through a negative effect of a drier atmosphere (Fig. 7.2) or indirectly through decreased internal plant water potentials as a result of drier soils (Fig. 7.3); there are many examples of both responses in the literature. Maximum values for stomatal conductance vary greatly for tropical trees, with the lowest values reported for *Eucalyptus urophylla* and *Eucalyptus cloeziana* (45 mmol m^{-2} s^{-1}) and the highest for values for *Tectona* (1340 mmol m^{-2} s^{-1}) (Table 7.1). Values for broadleaf trees are much greater than those for *Pinus*, including those species of pine widely planted in the tropics (e.g. *P. elliottii*).

The flux of CO_2 from ambient air through stomata is much less affected by partial stomatal closure than is the flux of water out of the leaf (Nobel 1991). Therefore, photosynthesis and stomatal conductance may not always be highly correlated, although they generally appear to be (e.g. for *Pinus:* Teskey et al. 1994b; for *Podocarpus:* Meinzer et al. 1984). Stomata have also been known to respond to CO_2, with conductances generally decreasing (Mott 1988; Eamus and Jarvis 1989). This response seems related more to changes in the concentration of intercellular CO_2 rather than to those of the ambient air.

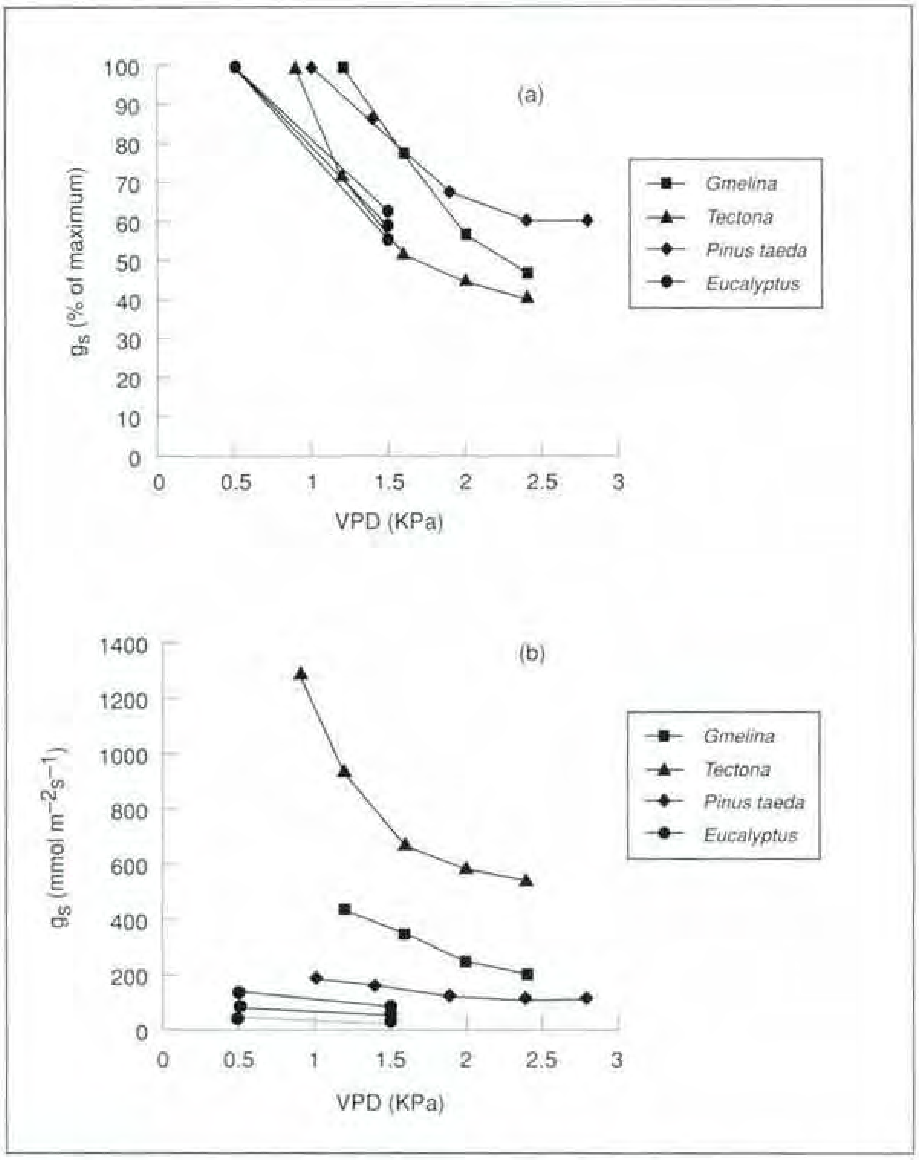

Figure 7.2 Stomatal conductance (g_s) in relation to atmospheric vapor deficit (VPD), (a) and (b) with the conductance in absolute units with conductance as a percent of maximum (data are from Pereira et al. 1987 for *Eucalyptus globulus*, Whitehead et al. 1981 for *Gmelina* and *Tectona* and Bongarten and Teskey 1986 for *Pinus taeda*)

The complex and sometimes counterintuitive responses of species to water availability were illustrated in a simulation study by McMurtrie et al. (1989). For Chiang Mai, Thailand, simulated carbon gain of *Eucalyptus* plantations increased with increasing L* in an environment where consistently high air saturation deficits led to generally low stomatal conductances. However, in such an environment, a species with a high conductance would not be able to prevent significant water stress without reducing L*. As a practical illustration of these results, there are many examples of very widely-spaced stands (extremely low L*) of *Eucalyptus* (and of other species) successfully planted in arid environments (e.g. Israel, Kenya).

Finally, many environments in the humid tropics are characterised by excess rainfall (i.e. precipitation is much higher than total evapotranspiration). Physiological effects of water-logging on trees are adequately reviewed elsewhere (e.g. Kozlowski 1984; Gliñski and Stepniewski 1985). However, the importance of excess soil water in limiting species' ranges, whether directly through effects on root functioning or physical damage or indirectly through increased pathogen susceptibility, should not be understated.

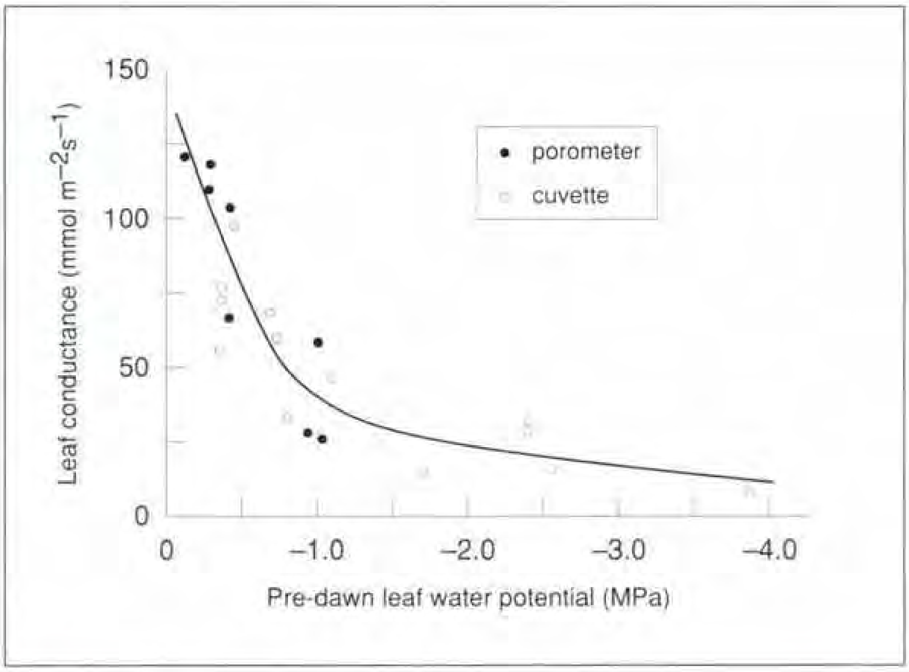

Figure 7.3 The relationship between maximum daily leaf conductance (g_s) and pre-dawn xylem water potential for *Eucalyptus globulus* (from Pereira et al. 1987)

Temperature

High air temperatures impose a direct energetic burden on a leaf which must be countered, for the most part through a combination of convective energy losses (H) and evapotranspirational cooling (λE). The Bowen ratio (ß) is a measure of this partitioning ($H/\lambda E$). With free water on canopy surfaces, ß approaches 0, or may even become negative if warmer air moves down into the canopy from aloft to balance the energy budget; the ß of a dry canopy with closed stomata (i.e. $\lambda E \rightarrow 0$) can become very large. For example, the mean ß for a dry tropical forest in Thailand varied from 0.45 during the monsoon season to 6.38 during the dry season (Pinker et al. 1980). Although it may be assumed that tree leaves operate near a ß = 1.0 on the average (i.e. that transpiration balances approximately half of the absorbed energy), in fact ß may be highly dynamic and is not well-characterised for forests in general. We could find no values in the literature of ß for tropical tree plantations, although the value of 1.0 is a good average for plantations of *Pinus elliottii* in Florida (Gholz, unpublished data). Since ß is relatively easy to measure, it has potential as a useful index of how various stands respond to environmental conditions in terms of relative water use.

The effects of ambient temperature on photosynthesis vary widely for tropical trees. Published values for the optimum temperature for photosynthesis of *Pinus* species are all at or below 30°C (Teskey et al. 1994b), although Teskey et al. (1994a) could not demonstrate a temperature optimum in the case of *P. elliottii* in Florida, even with air temperatures commonly over 35°C in the summer. Temperature optima, the growth-temperature acclimation of the optima, and differences in net photosynthesis at the optima were studied by Ferrar et al. (1989) for five species of *Eucalyptus*. They found that acclimation to different growth temperatures for photosynthesis varied, but that the responses could be aggregated into three groups that corresponded to the subgeneric groupings for *Eucalyptus*. The temperature optima for photosynthesis varied from 19 to 30°C; maximum photosynthesis rates also varied significantly (Table 7.1), but in no consistent pattern with growth or optimal temperature.

Nutrient availability

In natural ecosystems, species occurrences are obviously related to both soil nutrient availability and environmental characteristics (especially water status and temperature) of the site. White sand (Spodosol) soils are both dry (at least in the surface) and nutrient poor, and support distinctly adapted species over the entire temperature range, even when rainfall is abundant. In high montane forest zones it may be possible that soil nutrient availability is limited by effects of low temperatures on microbes; more widespread limitations would result from low water availability in dry environments with high temperatures. Some species may be able to counteract low inherent soil nutrient availability through N-fixation, deeper roots than native species, or more efficient use of nutrients. However, even-aged, closely-spaced plantations can exert an enormous demand for soil nutrients during the exponential phase of stand development, even for species on their native sites (Gholz and Fisher 1984).

Across a range in species, maximum photosynthesis rates are strongly related to leaf nitrogen concentrations (on either a surface area or mass basis (Chapin et al. 1993)). For example, Reich et al. (1994) found a positive linear relationship between A_{max} for native tropical tree species, which explained from 0.01 to 0.76 of the variation in photosynthesis across species from different Amazonian forest communities, as did Field and Mooney (1986), Evans (1989) and Zotz and Winter (1994) over a range of temperate C_3 species. However, direct effects of leaf nitrogen on photosynthesis within individual species vary, with the least evident effect in the conifers, especially among species of *Pinus* (e.g. Reich and Schoettle 1988; Teskey et al. 1994b), and the greatest effect in deciduous broadleaf species (Reich et al. 1992, 1994). Teskey et al. (1994a) found almost no relationship for mature needles of *P. elliottii*, although positive correlations have been found for other pine species (e.g. *P. sylvestris*, Smolander and Oker-Blom 1989). Mooney et al. (1978) found a very close relationship ($r = 0.97$) between maximum photosynthesis rates and leaf nitrogen concentrations (mmol g^{-1}) for six species of young (2- to 12- month-old) *Eucalyptus*. Leuning et al. (1991) and Pereira et al. (1992) found similar results for *Eucalyptus* growing under field conditions.

Foliar phosphorus (P) may also be an important regulator of photosynthesis in some species (e.g. *P. radiata*, Sheriff et al. 1986; Attiwill and Cromer 1982; Conroy et al. 1988; *P. contorta*, Reid et al. 1983). However, Mulligan (1989) found no effect of P deficiency on maximum photosynthesis of three species of *Eucalyptus*. Magnesium deficiency was also implicated in decreasing photosynthesis for the boreal *P. sylvestris* by Küppers and Schulze (1985). Information of the role of availability of nutrients other than N and P in affecting assimilation rates is largely absent.

Leaf development and aging may also influence photosynthesis, although this is confounded by the fact that most younger leaves have higher N and P concentrations. Reich et al. (1992) found that tropical tree species with higher leaf turnover times (shorter mean lifetimes) had higher N contents and photosynthesis rates. Also, leaves from seedlings and otherwise immature plants often have reported rates of photosynthesis higher than leaves from mature plants of the same species in the same light environment (Dougherty et al. 1994). Although the exact nature and cause of such relationships are not known for most tree species, models of carbon gain often incorporate a feedback between leaf N and photosynthesis (e.g. Running and Coughlin 1988; McMurtrie 1991).

Whether or not nutrition has an effect on photosynthesis *per se*, its effects on carbon allocation to stems and roots, on rates of respiration and on leaf area may be at least as important in regulating tree carbon gain (e.g. McMurtrie et al. 1994; see below). In general, it appears that trees on higher fertility sites allocate relatively greater proportion of carbon to above-ground parts (Vogt et al. 1986; Chapter 8).

Air pollution

Air pollution is an increasing problem worldwide with potential for adverse effects on the photosynthesis of tropical tree plantations in some locations. Effects vary by form of the specific pollutant, ranging from an indirect soil fertilisation effect from N deposited in precipitation (and in some rare cases, sulfur), to direct damage to leaf internal tissues and the photosynthetic apparatus by gaseous oxidants (e.g. O_3, SO_2, NO_x).

Evidence from the temperate zone suggests that almost all forest canopies are sinks for atmospherically deposited nitrogen, most in the form of soluble nitrate in precipitation. Results from an intersite study in North America (Johnson and Lindberg 1992) showed that canopy absorption of nitrate was proportional to the amount of nitrate deposition at the sites, and that canopy uptake of nitrogen was small compared to the annual nitrogen requirement of stands. Recent data from montane forests show elevated nitrate in cloud water and precipitation, probably a result of biomass burning and possibly high fertilisation of agricultural fields and subsequent degassing of nitrogen compounds in upwind, low elevation ecosystems. Clark (1994) demonstrated that significant amounts of cloud-enriched nitrate-nitrogen was absorbed and retained by bryophytic epiphytes in the canopies of tropical cloud forests in Costa Rica, but that leaves of native tree species and other vascular epiphytes were only weak sinks for nitrogen. At high concentrations, chemicals in mist solutions can damage leaf tissues. Valentini et al. (1989) found that simulated acid mist (pH = 3.5 and 2.2 *vs* 6.0 as a control) decreased net assimilation by *Eucalyptus globulus*, with recovery after several days observed at pH 3.5 level but significant necrosis occurring at the pH 2.2 level.

Nitrogen can also be taken up in gas form primarily as NO_2. In this case, uptake is proportional to stomatal conductance, so that broadleaf trees generally have a much greater potential for uptake than conifers (as well as potential for damage) (Hanson et al. 1988).

Direct damage by oxidants to leaves can occur as a loss of leaf area, through necrosis and/or premature shedding, or as a decrease in photosynthesis. Effects of chronic exposure on photosynthesis are generally proportional to the cumulative amount taken up, and so depend on the atmospheric concentration of the pollutant, the duration of exposure, the conductance of stomata and the capability of foliage to repair itself after damage (Reich and Amundson 1985). Evidence suggests that chronic ozone levels throughout eastern North America are sufficiently high to be causing reductions in the photosynthesis of almost all plants (Reich 1987). There is also some evidence to suggest that internal carbon allocation patterns are altered through exposure to ozone, even in the absence of visible leaf symptoms (Spence et al. 1990). In any case, there is a great deal of genetic variability in the responses of various species to the same levels of oxidant exposure (e.g.

Rutherford et al. 1993). In plantation management it may be possible to utilise this variability in selection programs for polluted sites. Although atmospheric pollution may not be of major importance to plantation productivity currently, increasing industrialisation in several tropical countries may eventually affect plantations.

Carbon dioxide concentrations of ambient air

The global average (i.e. including the tropics) atmospheric concentration of CO_2 is increasing rapidly (ca. 1.5 ppm yr^{-1}; Keeling 1986; Houghton et al. 1994), with potentially large but currently unknown consequences for tree growth. In addition to possible direct effects of increased CO_2 in the air, most general circulation models (GCM) of global climate patterns also predict that ambient temperatures in the tropics will change, although not as much in higher latitudes (Houghton et al. 1994). Recent reports suggest possible effects on the difference between day and night temperatures, which could alter tree carbon balances without affecting mean daily temperatures. The possible effects of altered temperatures on atmospheric humidity and rainfall amount and distribution are very important but currently very speculative as well.

In most assessments, the tropics are identified as a source of CO_2 to the atmosphere as a result of forest clearing and conversion to other land uses with less storage of carbon per ha (e.g. Houghton 1991). In addition, there is some evidence of a mid-latitude carbon sink, primarily through accumulation in regrowth (Tans et al. 1990; Houghton 1993). Recently, Grace et al. (1995) determined that a not-apparently disturbed, mature tropical rainforest in Rondonia, Brazil, was in fact also a significant net sink for atmospheric CO_2, while the general assumption has been that such ecosystems are 'carbon neutral'.

Whether or not the growth of existing forests is responding to the increasing atmospheric CO_2, through either direct stimulation of photosynthesis and/or decreases in respiration ('CO_2 fertilisation'), is highly controversial. Phillips and Gentry (1994) presented evidence of increased 'tree turnover rates' (defined as the difference between mortality rates and recruitment rates) of a range of mature tropical forests over the last decade, based on remeasurements of permanent plots. Direct effects of increased CO_2 on the growth of tropical tree plantations have not yet been reported.

The effects of ambient CO_2 concentrations on photosynthesis have been well-studied, but with inconsistent results (Eamus and Jarvis 1989). In the absence of other limitations, most studies of C_3 species indicate an initial rise in photosynthesis as a consequence of the increased substrate concentration for carboxylation by rubisco and a decrease in the oxygenase function of rubisco, which reduces photorespiratory CO_2 loss (Bowes 1991). This often results in a greater leaf area per plant and long-term gains in biomass. Many process-based models of NPP now contain effects of CO_2 on photosynthesis (e.g. McMurtrie et al. 1992).

However, in some species and conditions, increased efficiency per unit of leaf area is not maintained; rubisco amount, activity or activation state decline under long-term enrichment and the gain in biomass is mainly a function of greater leaf area alone. In other plants the improvement in efficiency is maintained and rubsico activity does not decline. There is apparently little or no acclimation by pines (Fetcher et al. 1988; Teskey et al. 1994b; but see Hollinger 1987). Stomatal limitations to photosynthesis in temperate and boreal tree canopies are generally low (e.g. 20% – 30% for *Pinus taeda*, Teskey et al. 1987), so that the potential for enhanced photosynthesis through further lowering of stomatal limitations seems low. This would be particularly true if long-term adaptations also included a decreased density and size of stomata (Eamus and Jarvis 1989).

A number of studies have found lower photosynthesis (measured at ambient CO_2 concentrations) in seedlings exposed to higher CO_2 levels (e.g. Oberbauer et al. 1985; Fetcher et al. 1988). This may be a result of assimilate accumulation in leaves and a 'feedback inhibition'. In contrast, the efficiency of nutrient use in photosynthesis should be greater with elevated CO_2, due to more efficient functioning of rubisco, translating to greater rates of carbon gain (Long and Drake 1991).

Incorporation of variable atmospheric CO_2 into models of forest production must account for effects at physiological, whole tree and ecosystem levels, in the face of often conflicting research results. McMurtrie et al. (1992) explored how this can be done using a set of four nested models. At the physiological level, photosynthesis was modelled in relation to the intercellular CO_2 concentration, the rate of carboxylation, the CO_2 compensation point and the rate of non-photorespiratory respiration (after Farquhar and von Caemmerer 1982). The response of simulated photosynthesis (at 25°C) to doubled atmospheric CO_2 ranged from 26% to 40% for leaves at low (less than saturated levels) and high (greater than saturated levels) of absorbed radiation, respectively. Modelled responses of annual production were much lower (8%) due to further limitations imposed by low soil nutrient availability.

A significant confounding factor is water stress. As already mentioned, effects of increased CO_2 concentrations, such as reduced stomatal conductance, may disproportionately affect transpiration and photosynthesis (Tolley and Strain 1984; Conroy et al. 1988). If photosynthesis is also directly stimulated, this would mean a greatly enhanced water-use efficiency and hence sustained productivity at lower levels of available soil water, although, again, large responses may not last in the long-term. Inconsistencies can also arise for experimental reasons. Most experiments on CO_2 effects have involved exposures of parts of mature trees (leaves, branches) or entire aboveground portions of immature trees in enclosures ranging from individual tree seedlings/cuttings in pots to groups of young trees in open-topped chambers. The use of immature experimental material is problematic

(Dougherty et al. 1994), although Coleman et al. (1993) argue that in many cases it may be irrelevant. More recent experiments in the temperate zone are focusing on free-air exposure (FACE) systems, although few results are yet available. In any case, except in the FACE studies, the above- and belowground environments of the trees are (sometimes greatly) altered compared to the natural environment, making results difficult to extrapolate.

Environmental alterations due to experimental conditions can include variations in the degree to which the plants can access soil nutrients and water, with many studies done under fertilised (high nutrient availability) and irrigated (low moisture stress) conditions. Short-term experiments usually find positive growth responses to enhanced CO_2 (Radoglou and Jarvis 1990; Norby et al. 1992), although this may be influenced by stage of development (Campagna and Margolis 1989). With nutrient limitations, as arguably occur in most forested ecosystems, it is not clear that above-ground growth responses to long-term elevated CO_2 will occur as internal carbon sink strength or low tissue nitrogen (or other nutrient) concentrations may be limiting. This may also be the factor contributing to low growth responses in many pot studies where root growth was limited (Arp 1991). This is further supported by results of Körner and Arnone (1992) using 'artificial ecosystems' of a mixture of tropical species (which incidentally included some of potential plantation importance), which demonstrated that CO_2 enrichment lead to greatly increased production and turnover of fine roots, with much lower increases in above-ground biomass and litter production.

Controls Over Respiration

The amount of carbon available for tree growth is further reduced from that fixed by the canopy due to respiratory losses for tissue maintenance. Net primary production, including that of roots, amounts to only 30 – 50% of annual canopy carbon gain (Ryan 1991). Little information exists on respiration, relative to photosynthesis, even though global warming and elevated CO_2 may significantly affect this critical process.

Respiration rates of tree tissues vary with the number of living cells and their metabolic activity. Ryan et al. (1994) recently reviewed the information available concerning dark respiration of *Pinus*. They found that needles and fine roots had similar specific respiration rates (nmol C (mol C biomass) $^{-1}$ s^{-1}), which were higher than those for woody tissues. However, because mature forests contain large amounts of wood, the contribution of woody respiration to stand carbon budgets can be substantial. Furthermore, rates for the same tissue tend to be higher for seedlings than for mature trees, which may be related to both a greater proportion of living cells and greater growth rates in the younger tissues of seedlings.

Metabolic rates of a specific tissue are primarily affected by temperature. Respiration, R, is usually expressed as a function of a 10°C change in air temperature, or Q_{10}:

$$R = R_0(Q_{10}{}^{t/10}), \qquad (2)$$

where R_0 is respiration at a temperature, t, of 0°C. In the short term, R_0 is generally regarded as a constant, although it can vary over periods of days to weeks in northern plants (e.g. Scholander and Kanwisher 1959), so that respiration rates at different temperatures can be much more similar than would be thought if based only on short-term measurements. Values of Q_{10} vary, but for all tissues centre on 2.0 (Amthor 1984; Ryan et al. 1994, although see Ryan 1990 for examples of values approaching 3.0 and Ryan et al. 1995 for values for stem tissues of <2.0). Cropper and Gholz (1994) used field-measured temperature responses of respiration for needles and fine roots of *P. elliottii* in a simulation study to explain lower L* values as a result of less net carbon available in Florida, with warmer night temperatures, than in more temperate South African sites.

Ambient CO_2 concentrations may also influence dark respiration (Baker et al. 1992; Idso and Kimball 1993; Bunce 1994; Wullschleger et al. 1994; but see Farrar and Williams 1991). In a review, Amthor (1991) concluded that higher CO_2 concentrations generally depressed respiration, although there has not been much work on trees on this subject. This issue is extremely important when approaches to measuring root respiration are discussed, as soil concentrations of CO_2 are much elevated compared to ambient air and are difficult to account for during measurements. Some evidence (Qi et al. 1996) suggests that estimates of fine root respiration made under field conditions on intact excavated roots (e.g. Cropper and Gholz 1991) may be flawed because they were made under CO_2 concentrations at the surface of the forest floor, not in the soil. In this situation, it may be more advisable to use approaches to quantifying root respiration that depend on partitioning of soil CO_2 fluxes (e.g. Raich and Nadelhoffer 1989), although Cropper and Gholz (1991) found that both approaches produced similar results for *P. elliottii* stands.

Respiration has also been related to tissue nitrogen concentrations (Ryan 1991) and several models contain such a dependency (e.g. McMurtrie et al. 1994). However, since field data are not adequate for full evaluation, this must remain hypothetical.

Air pollution (other than CO_2) may have various effects on tissue respiration rates (Amthor and Cumming 1988), and the evidence bears this out. On the one hand, tissue damage and decreased assimilation could lead to a decline in rates. On the other, the repair of tissues requires additional amounts of energy (at least on a temporary basis) and may lead to higher rates. The growth status of the plant and the nature of the specific pollutant are also likely to be important in determining responses (Amthor and Cumming 1988).

Respiration is usually partitioned into growth vs maintenance components, where growth respiration represents that used for construction of new tissue and maintenance respiration is that used for the repair and maintenance of existing tissue (Amthor 1989). This distinction, in higher latitude studies, has often been made through differences in field measured rates between dormant (non-growing) trees in winter and actively-growing non-dormant trees in other seasons (Ryan et al. 1995). However, in tropical climates with tree growth often occurring all year, this distinction may not be very useful.

Integrating Environment and Ecophysiology

Scaling from the leaf to the canopy

The successful extrapolation of measurements made on individual or small sets of leaves using small chambers up to the level of the whole canopy depends on how well the chamber environment resembles the ambient environment and how closely the leaf responses match changes in the environment. This coupling was formalised by Jarvis and McNaughton (1986) for water fluxes (transpiration), who introduced a factor, Ω, that depends on the ratio of the bulk aerodynamic conductance of a canopy to water vapour to the surface conductance of the leaves. Ω varies from 0 for tightly coupled canopies which are aerodynamically very rough, such as those with very small leaves (e.g. conifer needles) and a high degree of canopy turbulence (i.e. with high leaf boundary layer conductance), to 1 for canopies characterised by large leaves (e.g. *Tectona*) and a high degree of stability in the environment (with a low boundary layer conductance). Because photosynthesis is usually only weakly limited by stomatal conductance, and turbulence in forest canopies is relatively high (compared to other types of canopies, e.g. crop or pasture), it is generally assumed that small-chamber measurements (during which the air in the chamber is turbulently mixed, usually by a small fan) can in fact be scaled up to estimate canopy carbon gain.

Scaling up measurements is problematic for other reasons, particularly because stomatal conductance, photosynthesis and transpiration all depend on: 1) environmental conditions that often change greatly with position in the canopy; 2) species; and 3) leaves (e.g. of different ages) within a species. For small-chamber measurements to be extrapolated, huge numbers of observations must be made over a range of environmental conditions and throughout the canopy (including representation of different age classes, if present), even for mono-specific plantations (Beadle et al. 1985). The development of relationships (models) with environmental variables reduces the eventual amount of necessary field data. And in terms of photosynthesis, although the interactions of multiple-limiting factors are often difficult to conceptualise and represent mathematically, the pattern of incident light throughout the canopy is generally the factor that needs most accurate description.

Process-based, individual tree models (e.g. MAESTRO, Wang and Jarvis 1990) have been used to characterise the radiation regime and dynamics of canopy carbon exchange, which may be scaled to stand levels easily in even-aged, monospecific plantation stands (e.g. Leuning et al. 1991; McMurtrie et al. 1992; Teskey et al. 1994b). Even in these relatively simple situations, the data requirements are often staggering, limiting routine application. However, such models can be used for evaluating potential effects of differing canopy structure, phenology, tree spacing, environmental changes, pollution effects on photosynthesis, etc., over either short or long periods.

Stand-level models are an alternative, again primarily for stands with relatively simple structure and species composition (e.g. SPM, Cropper and Gholz 1993; BIOMASS, McMurtrie and Wang 1993). In these models, the canopy is usually depicted as a variable number of horizontal layers, so that simulations involving tree spacing and detailed variations in the crown structure cannot be reasonably simulated. However, they are relatively simpler to parameterise, e.g. with light attenuation in a layer represented through negative exponential relationships, while still containing process-level detail.

Recent technological advances now also permit accurate whole-ecosystem flux measurements for a variety of gases (e.g. CO_2, H_2O, CH_4 other hydrocarbons) to be made above forest canopies using sophisticated micrometeorological and gas analytical techniques (Beverland et al. 1996). Where the particular gas flux is controlled at only one main ecosystem surface, as in the case of water for otherwise dry canopies, comparisons between scaled-up small chamber estimates of transpiration can be made with the above-canopy flux measurements. Where agreement is high, models can be reliably extended in their application. So far, this seems to be a more cost-effective and logistically possible approach to obtaining regional or multipoint flux estimates, when compared with attempts to actually replicate above-canopy tower-based measurements. However, in the case of CO_2, the interpretation of above-canopy flux measurements becomes extremely difficult without detailed within-ecosystem information on the numerous sources and sinks.

Scaling from the canopy to the whole stand: internal allocation of fixed carbon

Models such as MAESTRO and BIOMASS have generally been used to simulate the seasonal net carbon exchange of the crowns of individual trees or whole stands. The outputs from these models include net carbon gain, from which all tissue maintenance, growth, replacement and protection, as well as the production of reproductive materials, must come (Fig. 7.4). The controls over carbon allocation to various tissues and functions within a tree are complex and involve the coupling of carbon, water and nutrient balances. Our understanding of the mechanisms is very incomplete, and numerous alternative models exist (see review by Dewar et al. 1994 for pines).

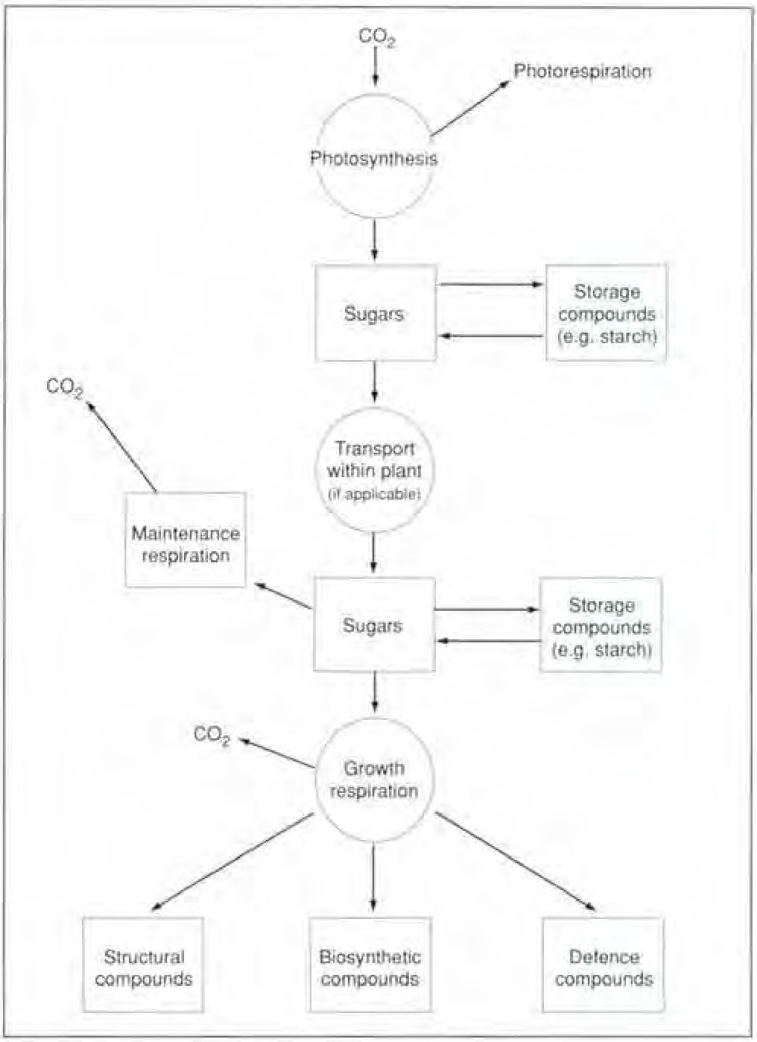

Figure 7.4 Conceptual model of internal carbon allocation within trees (from Margolis and Brand 1990)

Stemwood biomass accumulation is often regarded as a residual of this allocation, after root systems and above-ground respiration have been subtracted (Waring and Schlesinger 1985). Although widely accepted, there are few, if any, studies that have simultaneously measured enough of the other carbon fluxes for this concept to be verified experimentally. There are numerous examples where simulated stem growth is compared to that observed in field plots as a measure of model performance (e.g. Cropper and Gholz 1993), but matchups could always be fortuitous.

Within a tree, there is a dynamic balancing act taking place, with continuous regulation at the biochemical and molecular levels. Factors both internal and external to the tree can affect carbon allocation. Genetics obviously sets limits to the eventual form and physiological functioning of a species, although considerable variability is possible. As an example of an external effect, CO_2 enrichment enhances carbon acquisition. As a consequence, this may be reflected by acclimation (both up- and down-regulation) in fluxes and enzymatic activities associated with a wide range of physiological processes. These include: 1) photosynthetic electron transport; 2) photosynthetic carbon reduction and photorespiratory carbon oxidation (PCO) cycles; 3) cellular respiration; 4) carbohydrate, protein and secondary metabolism; and 5) the acquisition and utilisation of water and nutrients, nitrogen and phosphorus in particular, from the soil. These biochemical changes produce a cascade of positive and negative feedbacks that ripple through all levels of the system, from the physiology and anatomy of the tree to the whole ecosystem.

For example, if a decline in aboveground respiration occurs under elevated CO_2 conditions, it may result in an increase of the root:shoot ratio. Growth under elevated CO_2 conditions often changes the allocation patterns for fixed carbon, both at the biochemical level and whole plant level. Thus, carbon may be diverted away from the PCO cycle while production of carbohydrates, especially of starch, may be favoured over protein (Stitt 1991). Although the consequences for defensive chemical production and ecosystem processes such as root detrital production and decomposition could be substantial, the regulatory processes for such phenomena are poorly understood.

An alternative to more mechanistic approaches to modelling internal carbon allocation is the use of optimisation models (Dewar et al. 1994). King (1993) used the basic model proposed by McMurtrie (1991) to model carbon allocation in relation to nitrogen availability for even-aged conifer plantations under limited soil nitrogen but adequate soil water conditions. This more 'functional analysis' of allocation balanced the carbon costs for a particular allocation strategy against the benefits of nutrient and carbon acquisition (see also Eissenstat and VanRees 1994). Results of these analyses support field observations that trees allocate more carbon to roots when nutrients are limiting and that species adapted to nutrient-poor sites usually have longer-lived foliage.

Other possibilities exist for feedbacks on carbon allocation from roots to shoots, besides a general response of trees to low nutrient availability. For example, Reis et al. (1989) demonstrated that root restrictions imposed by varying pot sizes on three species of *Eucalyptus* not only affected resultant height and diameter growth, but that the species which exhibited sensitivity in the first part of the study continued with lower subsequent growth even after root restrictions were lifted (see page 244).

Efficiencies of Water and Nutrient Use

The potential dry matter production of a forest plantation, a function of the amount of radiation intercepted by the canopy, may be restricted by both water and nutrient stresses (Chapters 3 and 6). The efficiencies of the use of these two environmental resources by trees can be seen as important plant adaptative mechanisms of coping with water and nutrient scarcity. Water-use efficiency (WUE) and nutrient-use efficiency (NUE) can be variously expressed, and a great degree of confusion exists among terms and specific units of measurement (Grubb 1989). Expressions and discussions have ranged from the level of a single leaf to that of a stand, using a range of measures of productivity.

Nutrient-use efficiency

In this review, we mainly discuss the concept using nitrogen in reference to NUE, mainly because of the lack of information for other nutrients, but also because inadequate nitrogen supply is a well-established limitation in plantations of the temperate and boreal latitudes. Although much of the discussion should be generally applicable in concept, nutrient availability in soils and use by plants varies considerably so that such generalisations should be viewed with caution.

Instantaneous photosynthetic nutrient-use efficiency (NUE_i) can be expressed as the rate of CO_2 uptake per unit of nutrient invested in leaf tissue (Field and Mooney 1983). If a tree responds to a non-nutritional environmental stimulant (e.g. elevated CO_2) through an increase in growth, it may exhibit 'N-sparing', with less NO_3-N and organic-N in the tissues and less protein, especially in rubisco, thereby increasing its NUE_i. Concomitantly, the enzymes (including nitrate- and nitrite-reductases) involved in nitrogen metabolism, whether root or shoot, may decline. Decreased dark respiration as a possible result of CO_2 enrichment should further increase NUE_i, especially if respiration and nitrogen concentrations are not closely coupled. In practice, NUE_i is difficult to determine given that photosynthesis may vary rapidly while nutrient concentrations can generally only be measured periodically.

NUE_i data for tropical trees are relatively scarce. Values for species mostly used in plantations fall within the range of 0.02 to 0.07 (Table 7.2). Four of the five *Eucalyptus* species from Mooney et al. (1978) exceed 0.05, and *Pinus elliottii* is at the low end of the range. The range from the study by Reich et al. (1994) for natural forest species is from 0.02 to 0.07. NUE_i has been shown to be higher at lower levels of nutrient availability, a pattern also observed for *Eucalyptus grandis* (Mooney et al. 1978) and *P. elliottii* (Table 7.2).

Most plantation tree species are extremely conservative of soil nutrients in relation to their productivity. But where productivity is high, the demand for soil nutrients is also high in any case. For example, *Eucalyptus* species have generally high plant-level NUE (NUE_p), but because they also are generally very productive, they still exhibit very high soil nutrient uptake rates (Chapter 12).

Water-use efficiency

Similar to NUE, WUE can be expressed on an instantaneous basis or over a longer period. However, WUE_i is generally much easier to determine than NUE_i, because CO_2 and water fluxes are often measured together at the same temporal and spatial scales using small-chamber approaches.

Table 7.2 Net photosynthesis (Pn), leaf N concentrations ([N]) and their ratio (Instantaneous nutrient-use efficiency, NUE_i)

Species	Pn (mmol CO_2 m^{2} s^{-1})	[N] (mmol m^{-2})	NUE_i	Reference
Aspidosperma album	4.0	93	0.043	Reich et al. 1994
Cecropia spp.	3.0	93	0.032	Reich et al. 1994
Cecropia spp.	13.0	136	0.022	Reich et al. 1994
Ceiba pentandra	7.0	125	0.056	Zotz and Winter 1994
Eucalyptus blakelyi	6.1	271	0.023	Mooney et al. 1978
E. maculata	9.1	157	0.058	Mooney et al. 1978
E. melliodora	6.7	121	0.055	Mooney et al. 1978
E. pilularis	5.8	93	0.062	Mooney et al. 1978
E. saligna	3.7	50	0.074	Mooney et al. 1978
Miconia spp.	5.8	89	0.065	Reich et al. 1994
Ocotea spp.	6.0	136	0.044	Reich et al. 1994
Pinus elliottii (fertilised)	2.5	88	0.028	Teskey et al. 1994a
P. elliottii (control)	2.5	65	0.039	Teskey et al. 1994a

Table 7.3 Instantaneous water-use efficiency (WUE_i)

Species	WUEi ($mmol\ CO_2\ mmol\ H_2O^{-1}$)	Reference
Cambretum quadrangulare	2.2	Luangjane 1990
C. quadrangulare [c]	0.5	Luangjane 1990
Ceiba pentandra	3.0	Zotz and Winter 1994
Erythrina variegata	4.9	Muthuchelian et al. 1989
Eucalyptus camaldulensis	2.5	Luangjane 1990
E. camaldulensis[c]	0.9	Luangjane 1990
E. camaldulensis	3.8[d]–5.7[e]	Lima and Jarvis, unpublished data
E. globulus	7.0	Pereira et al. 1986
E. grandis	4.1[d]–6.9[e]	Lima and Jarvis, unpublished data
E. maculata[a]	6.7	Wong and Dunin 1987
E. maculata[a]	5.0	Denmead et al. 1993
E. maculata[b]	4.1	Denmead et al. 1993
E. pauciflora	7.5	Küppers et al. 1986
E. phaeotrica	3.7[d] –7.0[e]	Lima and Jarvis, unpublished data
E. torelliana	3.9[d]–6.9[e]	Lima and Jarvis, unpublished data
E. urophylla	4.6[d]–6.3[e]	Lima and Jarvis, unpublished data
Larix eurolepis	5.5	Sandford and Jarvis 1986
Picea sitchensis	6.0	Sandford and Jarvis 1986
Pinus contorta	4.4	Sandford and Jarvis 1986
P. radiata	2.0–3.5	Sheriff et al. 1986
P. sylvestris (old)	3.9	Sandford and Jarvis 1986
P. sylvestris (new)	4.0	Sandford and Jarvis 1986
P. taeda	3.0–4.4	Fites and Teskey 1988
Podocarpus oleifolius	4.8	Meinzer et al. 1984
P. respigliosii	3.4	Meinzer et al. 1984

[a]Trees enclosed in tents; [b]Forest; [c] Under 2% salinity; [d]Ambient CO_2; [e]Elevated CO_2 (double ambient)

Given the large number of species just of *Eucalyptus*, there are surprisingly few published data on the gas exchange patterns of tropical plantation species, so that generalisations regarding WUE_i are difficult to make even for this single important genus (Lima 1993). Nevertheless, a compilation of the available studies, including data for tropical tree species used in plantations in tropical regions as well as some for a few other tropical tree genera and some temperate tree species as a comparison, shows interesting trends (Table 7.3). The overall range in WUE_i is from about 2.0 to 7.5 μmol CO_2 mmol H_2O^{-1}, with the values tending to form a few groups with comparable ranges. For example, WUE_i values for *Eucalyptus* species fall in the upper part of the range for all species (under ambient conditions). The results also show a significant increase in WUE_i with increasing CO_2 concentration and a marked decrease with soil salinity stress.

Eucalypts are, by far, the most commonly used tree species in tropical plantations and are currently the centre of controversy, attributed with abnormally high rates of water consumption. Such rates could be associated with high growth rates, low WUE, or both. However, given the large number of species in the genus, it is not surprising that there is significant variation among them in terms of stomatal anatomy, acclimation and other morphological and physiological characteristics which could affect their use of water (Ladiges 1975; Slatyer and Ferrar 1977; Carr and Carr 1978). A review by Lima (1993) indicates that two sub-genera of *Eucalyptus* may be characterised by widely different water-use strategies. This may lead to a more functional grouping of species in future studies, making possible more informed and simpler species selection for particular environments.

The question of whether the eucalypts, or any other fast-growing tree species, produce more biomass per unit of water consumed as compared to other tree species is of considerable practical interest. Absolute values of water requirements for wood production are difficult to obtain under field conditions. Nevertheless, there are some values from field studies and more which can be calculated from published data (Table 7.4). It can be seen from these few results that plantation eucalypts average around 2.6 g biomass produced kg^{-1} of water consumed (using the minimum value from Olbrich et al. 1993, the range of which represents different clones of *E. grandis*), which is higher than the corresponding values for *Pinus caribaea* and the other tropical tree species. The results by Eastham et al. (1990) show a clear increase in WUE with increasing tree density (with a value of 1.3 at 82 trees ha^{-1}), probably because L_* stabilises (thus limiting further increases in water use) while biomass increment continues to increase with more stems.

Finally, if stomatal conductance is lowered by increased CO_2 concentrations, such a response can to some extent compensate for a stimulation of photosynthesis, but more likely will reduce transpiration (Jarvis 1987). The integrated effect is the generally-observed increase in WUE (Oberbauer et al. 1985; Eamus 1991;

Table 7.4 Plant level water-use efficiency (WUE_p)

Species	WUE_p (g biomass kg^{-1} H_2O)	Reference
Acacia auriculiformis	1.2	Chatuverdi et al. 1988
A. nilotica	1.3	Chatuverdi et al. 1988
Albizia lebbek	1.7	Chatuverdi et al. 1988
Eucalyptus globulus	2.0	Pereira et al.1986
E. grandis	3.0– 6.1[a]	Olbrich et al. 1993
E. grandis (2150 stems ha^{-1})	4.6	Eastham et al. 1990
E. grandis (304 stems ha^{-1})	1.9	Eastham et al. 1990
E. grandis	2.9	Lima et al. 1990
E. maculata	2.3	Wong and Dunin 1987
E. tereticornis	1.9	Chatuverdi et al. 1988
Pinus caribaea	2.1	Lima et al. 1990
P. caribaea	1.3	Waterloo 1994
Prosopis juliflora	1.4	Chatuverdi et al. 1988

[a] Variation among four clones

Ziska et al. 1991). For example, Lima and Jarvis (1995) and Lima et al. (1995) found that stomatal conductance decreased significantly over a 5-day drying cycle for five species of *Eucalyptus* under both ambient and doubled CO_2 concentrations, whereas photosynthesis was maintained at a significantly higher level for elevated CO_2 plants over the entire time (Table 7.1; see also Colquhoun et al. 1984; Chaves and Pereira 1992). However, increases in leaf area may offset such increases in WUE and still lead to higher rates of transpiration at the stand level (at least if L_* is not so high that all the light is already intercepted). Interpretation of NUE and WUE over long-term, stand-level conditions presents an array of complex issues, and caution is required in the simplistic application of these concepts in a management context.

Synthesis

A conceptual framework exists for the interpretation of physiological data in the context of understanding the environmental controls over productivity of tropical tree plantations. In addition, numerous computer models of forest productivity exist which incorporate physiological processes to varying degrees (e.g. Dixon et al. 1990; Kaufmann and Landsberg 1991). However, this review found that the data appropriate for parameterising such models for tropical trees is generally scarce, with most information available only for the two currently dominant genera of *Pinus* and *Eucalyptus*. There is no published information concerning most native species, some of which may have high potential for plantation use.

Beyond data availability, there still are significant limitations on the usefulness of physiological data and physiologically-based models in addressing day-to-day forest management issues. The main scientific issue (not restricted to the understanding of tropical trees) is how, during photosynthesis, the partitioning of carbon fixed among various tree tissues is controlled. This has limited model development primarily to the canopy level (McMurtrie et al. 1994), except where major assumptions are made about allocation which limit the credibility of resultant models.

A second key limitation has been the inability to validate model results. In this case, recent technical advances now allow relatively easy (albeit expensive) measurements of whole-forest fluxes of CO_2 and water. This means that stand-level predictions of carbon and water fluxes from models based on process-level information should increasingly be able to be quantitatively evaluated. On the other hand, stand-level carbon flux measurements by themselves will not be very useful without an associated understanding of the controls over the fluxes. However, research is still derived mainly from relatively few, diffuse and largely uncoordinated projects and programs. It must be recognised that collection of data on the rates and controls of particular physiological processes, or stand or ecosystem fluxes, in isolation will not contribute greatly to the resolution of this situation, given often irresolvable differences in methodologies and research contexts (e.g. species and developmental stage, environmental conditions).

Therefore, although some major issues such as the relative use of water by highly productive trees and stands of *Eucalyptus* in comparison with other tree species and competing land uses (e.g. Calder et al. 1992) are resolvable, the debates will continue. Real progress in the development and application of models to the prediction of productivity will result only when physiological, environmental, and stand gas flux data are more systematically collected as integral parts of studies addressing the growth of tropical tree plantations. There has been enormous progress in developing methodologies for studying ecophysiological processes, from the level of tissues to stands, through research in temperate forest ecosystems. These methodologies can be adapted to build appropriate research in the tropics.

Acknowledgments

This project was mainly completed while Gholz was an American Association for the Advancement of Science (AAAS), Science and Engineering Diplomacy Fellow at the U.S. Agency for International Development (Bureau for Global Programs, Field Support and Research, Center for Environment). He expresses gratitude to Michael D. Benge, Senior Agroforestry Advisor at the Agency for generous support during the Fellowship.

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8

Roots and Mycorrhizas in Plantation Ecosystems

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Abstract

The role of roots and mycorrhizas in natural and plantation forests in the tropics is reviewed. To illustrate key issues that need to be considered when trying to assess the role of roots and mycorrhizas in tropical forest plantations, literature from the temperate zone is used when information is not available from the tropics. The following characteristics of roots and mycorrhizas are reviewed: root diameters and their function, root density and nutrient uptake, rooting depth, fine root seasonality, root adaptations, types and distribution of mycorrhizal associations, mycorrhizal attributes, and variability in host plant and fungus relationships. Other topics reviewed are: 1) tree productivity, carbon allocation within trees and what controls allocation to roots plus mycorrhizas and shoots, 2) how the importance of roots and mycorrhizas varies with stand development and succession, 3) the relationships between roots and mycorrhizal associations and nutrient cycling, and 4) how roots and mycorrhizal associations need to be considered in forest management (specifically focusing on fungal pathogens and insect pests, heavy metal toxicity and several management activities). Research topics that are important to pursue to better understand the role of roots and mycorrhizas in forest plantations are presented throughout the text. The rationale is presented for using an ecosystem approach, rather than isolated studies, when examining roots and mycorrhizas.

MOST RESEARCH on tropical plantations has emphasised those factors that would assist survival of seedlings planted at a site, those parts of the ecosystem that were thought to have the strongest influence on the wood growth of trees, or the effects of harvesting trees on environmental site conditions. These studies have been very useful for developing management tools to increase wood growth of plantation species, for producing techniques that guarantee the regeneration of the desired species and for minimising erosion and nutrient losses from sites after harvesting. In addition to these factors, there is a real need to understand the role of roots and mycorrhizas in acquiring nutrients and water in plantations since the latter factors control carbon allocation patterns within plants and the achievable productivity on the site. Frequently roots and mycorrhizas have not been included in studies because of the difficulties of collecting and processing data on something that is not visible. The emphasis in the ecological literature has been to identify surrogate ecological parameters that can be measured aboveground or to model carbon allocation to root growth (Vogt et al. 1986; Raich and Nadelhoffer 1989; Santantonio 1990;

Landsberg et al. 1991; Cannell and Dewar 1994). The database on fine roots and mycorrhizas for plantation ecosystems in any climatic zone is small (Nambiar 1983; Gholz et al. 1986; Vogt 1987; Fabiao et al. 1990/91) and few data are available from tropical and subtropical plantations (see Tables 8.1–8.4 on pages 266–278; Cuenca et al. 1983; Singh and Srivastava 1984; Santantonio and Santantonio 1987; Cuevas et al. 1991; Montagnini et al. 1991; Lugo 1992; Parrotta 1992; Parrotta and Singh 1992; Montagnini 1995). Most research on plantations has focused on aboveground parts.

We are beginning to understand the role of fine roots and mycorrhizas in the ecosystem-level response of forests to a changing environment (Allen 1991; Vogt et al. 1993). Since intensive management of plantations has the goal of increasing the growth of specific parts of a plant as the desired product, we need to understand the implications of a management activity imposed on part of the system and how this affects plant carbon allocation between the shoots and roots in both the short and long terms.

Improved understanding of belowground response to management requires studies with a holistic approach that considers roots and mycorrhizas as an integral part of the ecosystem. We frequently do not know the feedbacks in ecosystems, so it is wise not to ignore a large part of a system. It is equally critical that studies of belowground parts of ecosystems do not ignore the rest of the ecosystem. The consequences of not taking a holistic approach are often severe: ecosystems may become more susceptible to insects and disease, to moisture and/or nutrient stress, and ultimately have decreased production. Since management practices are intended to accelerate aboveground growth, we have to understand how the same practices influence the resistance of plants to disturbance.

Whether the major concern is carbon and nutrient cycling rates, net primary production or plant response to and their rate of recovery (i.e. resilience) after a disturbance, there are certain fundamental issues of the belowground environment which should be considered. For example, the contribution of roots to controlling/regulating carbon and nutrient cycling rates and stand production must be understood because roots acquire nutrients from the soil and they may contribute significantly upon their senescence to decomposition and nutrient mineralisation (Vogt et al. 1986). Symbionts (mycorrhizal associations) are particularly important to studies of plant responses to disturbance (Vogt et al. 1993) since seedlings without the interface that mycorrhizae provide between the plant and the soil grow poorly (Harley and Smith 1983; Perry et al. 1987).

This chapter addresses the role of the belowground ecosystem in maintaining the productivity and health of plantations, focusing on roots and mycorrhizae. In particular, we explore the following questions: What do we presently understand about the belowground ecosystem in tropical plantations? How may belowground processes in tropical plantations be connected through feedback mechanisms to overall ecosystem health and function? How can the management of and research on tropical plantations incorporate an ecosystem approach which integrates both above and belowground processes? This chapter does not provide a comprehensive review of existing knowledge on belowground systems in tropical plantations. The objective is to provide a framework of available information for analysing questions about roots and mycorrhizas, and suggest how these questions should influence research and management of plantations.

Role of Fine Roots and Mycorrhizas in Forest Ecosystems

The following section will present general information on roots and mycorrhizal associations as a basis for developing research in plantations. We have used information from the temperate zone to illustrate key issues, but similar processes are likely to occur in the tropics.

Root characteristics

Root diameter and function

The functional attributes of roots are influenced by root diameter: 1) fine roots (including mycorrhizal associations) <2 mm in diameter comprise most roots involved in nutrient uptake; 2) small to medium roots >2 mm in diameter function in transport and storage of carbohydrates and nutrients; and 3) coarse and primary tap roots provide anchorage for the plant, resist stand damage from wind and snow, and take up water from deeper sources in areas with seasonal precipitation. Typically researchers have collected data on only one or two of these size classes to illustrate a particular aspect of root growth. Studies on roots should carefully consider the size class chosen for analysis.

The mass of root systems (or their components) does not fully reflect their functional role or how much carbohydrate is translocated to maintain them. The fine root class comprises a very small fraction of the total weight of the root system: in the temperate zone, typically less than 5% of the total weight of the total root system is in fine roots even though up to 90% of the length of the total root system and over 90% of the root turnover is in this fraction (Bowen 1984; Vogt et al. 1989). Furthermore, in a subalpine environment in the temperate zone, 13 excavated *Abies amabilis* trees that were 30 yr of age had 3.8% of the total root dry weight in the 1–2 mm diameter class while 19.1% of the root surface area was in this class (Vogt et al. 1989). In contrast, for these same trees, the primary supporting root accounted for over a third (34.4%) of the total root weight but only 5.6% of the entire root surface area (Vogt et al. 1989).

The amount of carbon allocated to roots appears to vary with the plant spacing (Puri et al. 1994). In a desert region in India, Puri et al. (1994) recorded that the proportion of total root biomass in fine roots increased from 30 to 75% when the spacing of *Populus deltoides* trees increased from a 2 × 2 m to 6 × 6 m, respectively. Furthermore, trees growing under wider spacing allocated more total carbon to their roots compared to those with the narrower spacing.

Coarse roots have been effectively incorporated in biomass studies because this biomass can be predicted from allometric regressions incorporating tree diameter at breast height (Santantonio 1990). Even though fine roots and mycorrhizal associations are maintained by carbohydrate fixed in leaves, it has been difficult to identify aboveground parameters that can be used to predict how much carbon is allocated to root growth and maintenance. Fine roots and mycorrhizal associations respond at the microsite scale that is very different from the response of the whole root system (Friend et al. 1990; Pregitzer et al. 1993; Roy and Singh 1995). The overall position is further complicated by the fact that while the presence of the symbionts on root systems may be costly (~15% of total Net Primary Production, NPP, is allocated to symbiotic associations), since the symbionts increase the longevity of the fine roots the actual cost of maintaining these roots may be much reduced when amortised over annual time scales (Vogt et al. 1982). It is critical that we understand the dynamics of fine root mycorrhizas since they respond to a plant's changing resource availability.

There is no relationship between the measured mean annual fine root biomass and annual fine root NPP. These differences are highlighted in a comparison of a secondary wet tropical forest with adjacent *Pinus caribaea* plantations in Puerto Rico (Cuevas et al. 1991). In this plantation less than 1% of the total biomass was in fine roots compared to 6% of NPP in fine roots (Cuevas et al. 1991). The secondary forest had an even more dramatic difference between biomass and NPP—9% of total biomass and 44% of total NPP was in fine roots. These comparisons were made in forests that were both 11 yr of age. They exemplify the substantial differences which may occur between species in allocation of resources to fine roots to acquire the nutrients required for growth.

Root density and nutrient uptake

Since nutrient uptake by plants is more a function of the root surface area than root weight, root weights by themselves are difficult to convert to a useful index of plant ability to take up nutrients (Nambiar 1985). Root density (i.e., root length per given volume of soil) measurements are a more useful indication of plant ability to access soil nutrients. For example, Barley (1970) originally developed soil nutrient depletion curves that related rooting density to the mobility of soil nutrients (e.g., highly, poorly or non-mobile). This type of analysis makes it possible to determine whether the rooting density is adequate to access the nutrients required for growth.

As part of the nutrient depletion curves, the optimal rooting densities had to be greater than 2 cm cm^{-3} for taking up the highly mobile elements nitrate and sulfate, while a rooting density greater than 4 cm cm^{-3} was required for the poorly mobile elements (Barley 1970; Nambiar 1985). Actual rooting density measurements for *Pinus radiata* were 0.13–0.18 cm cm^{-3} when seedlings were 3–4 yr old, 1.1–2.9 cm cm^{-3} when 8 yr old and 2 cm cm^{-3} at 14–16 yr of age (Bowen 1984; Nambiar 1985). It is obvious that these values are much lower than those desirable for accessing poorly mobile and non-mobile elements, and therefore the role of mycorrhizae in facilitating nutrient uptake must be considered. In other cases, mycorrhizas may not be as important in contributing to increasing root densities since plant root densities are effective at acquiring even the most non-mobile nutrients. For example, 11-yr-old *Eucalyptus marginata* had a rooting density of up to 7 cm cm^{-3} (Carbon et al. 1980) which based on Barley's (1970) nutrient depletion curves would be very effective in absorbing poorly mobile nutrients such as P from the soil.

Under field conditions, mycorrhizal hyphae or rhizomorphs significantly increase the surface area of plant root systems accessible to poorly or immobile elements like ammonium, phosphate, copper and zinc. However, as measurements of the extent of hyphal development in the field have not been well documented the significance of the contribution by hyphae to nutrient uptake cannot be quantified. Interestingly, in subalpine *Abies amabilis* ecosystems in Washington, USA, extensive hyphal networks were observed when soil fluxes of poorly mobile nutrients were greatest and when fine root growth was the most active (Vogt et al. 1982). Roy and Singh (1995) observed a similar direct correlation between root growth and mineral nitrogen in a dry tropical forest. These studies suggest that the timing of N mineralisation and growth of roots and associated fungi is synchronous—an effective adaptive mechanism for conserving nutrients in forest ecosystems.

Rooting depth

Many studies of the success of mixed-species plantings have collected information on rooting depth for each species (Alpizar et al. 1986; Jonsson et al. 1988; Young 1989; Dhyani et al. 1990; Fassbender et al. 1991; Opakunle 1991). In addition to revealing how much of the soil space is occupied by roots, rooting depth information is particularly useful in the tropics since large areas of the those forests experience short- to long-term seasonal droughts. Growth of plantations in areas with dry periods is facilitated if deep-rooted tree species are selected to use deeper sources of water. It has been shown that deep-rooted plants may bring up water from deep sources and make it available to other plants growing in their space (Richards and Caldwell 1987; Caldwell and Richards 1989). This ability may be a useful criterion to use when selecting the combination of trees to grow together in a mixed plantation, but one has to careful that these species do not over-utilise water resources.

Stone and Kalisz (1991) have synthesised information on the maximum rooting depths for tree species—mostly for the temperate zone. Most plants appear to have rooting depths that average 1–2 m. Bowen (1984) reported *Eucalyptus marginata* rooting to 1.6 m while Dhyani et al. (1990) reported values of 4.2 m for *Eucalyptus tereticornis* and 2.8 m for 28-month-old *Leucaena leucocephala*. Deep-rooted Amazonian semi-evergreen forests have been reported to have maximum rooting depths of 12 m (Stone and Kalisz 1991), while the greatest root depths (consistently exceeding 35 m) were reported for several eucalypt species, *Acacia raddiana* and *Prosopis juliflora* (a desert shrub). The maximum rooting depth reported for any plant species was for *Eucalyptus* sp. which had roots going to 60 m.

Fine root seasonality

There are seasonal patterns of root growth in coniferous and deciduous forests in the temperate zone (Harris et al. 1977; Vogt et al. 1982; Aber et al. 1985; Vogt et al. 1986; Santantonio and Santantonio 1987). In the cold temperate zone, seasonal peaks of higher root biomass occur immediately before or after the period of high shoot growth—typically drawing on stored carbohydrate in early spring and current photosynthate and stored carbohydrate in the autumn. For example, 40-yr-old *Pseudotsuga menziesii* growing in the temperate zone had fine root production directly correlated to the starch content of phloem tissues in the bole (Vogt et al. 1985).

Similar seasonal cycles (i.e. modal or bimodal) of fine root growth have been reported in the tropics. In seasonally-dry tropical forests in India, fine root biomass varied seasonally from about 700 to >2000 kg ha^{-1} at 20–40 cm depth (Singh and Srivastava 1985) and from 1740 to 3740 kg ha^{-1} (Roy and Singh 1995). In wet humid tropical forests in Puerto Rico, fine root biomass ranged from 200 to 8000 kg ha^{-1} (Cuevas et al. 1991; Kangas 1992; Vogt et al. 1995a).

Disturbance may reduce the seasonal peak of fine root biomass. For example, following hurricanes with several year drought cycles in the Caribbean (Scatena, International Institute of Tropical Resources, Puerto Rico), the standing crop of fine root biomass was 2400 kg ha^{-1} (Vogt et al. 1995a) compared to previously reported values exceeding 8000 kg ha^{-1}. In the same forest, Kangas (1992) recorded a fine root biomass (<5 mm) of 8186 kg ha^{-1} during a non-hurricane period. Because fine roots turn over at least once annually (Vogt and Bloomfield 1991), the data presented by Cuevas et al. (1991) also suggest that it is not unrealistic to have a difference of 8000 kg ha^{-1} in seasonal fine root biomass in the humid tropics which is comparable to reported values in the cold temperate zone (Vogt 1991).

In the wet and dry tropical forests, short-term (i.e. weeks) dry periods appear to have strong influences on the timing of root turnover and periods of fine root growth. In tropical dry forests, moisture availability controls the timing of fine root growth (Singh and Srivastava 1985; Kavanagh and Kellman 1992). Singh and Srivastava (1985) reported a bimodal pattern of root tip growth of *Tectona grandis* plantations in seasonally dry areas that was regulated by moisture availability. This is similar to a dry tropical forest studied by Roy and Singh (1995) which also showed a modal pattern of fine root growth. Even in humid tropical forests, fine root growth is controlled by short periods of low or no precipitation. In a humid tropical secondary forest in Puerto Rico, a modal cycle of root growth occurred where the seasonality was controlled by annual dry periods several weeks long (Vogt et al. 1995a). It is therefore critical to determine the periodicity of root growth so that sampling can effectively detect this variability.

Most of the studies in the tropics on plant species for agroforestry or multiple-tree species systems have used a one-time sampling period to determine differences between the root biomass of species (Table 1). Because there are seasonal patterns of fine root growth, variation between species in the timing and cessation of fine root growth, and variation in root growth by depth in the soil profile (Ford and Deans 1977; Vogt et al. 1995a), one-time sampling without information on temporal changes should be avoided. The lack of significant differences in fine root biomass (531–780 kg ha^{-1}) between four tree species grown in combination with an agricultural crop (Jonsson et al. 1988) could be related to the time period in which root cores were collected. In this case, seasonal data on root biomass might have shown differences in fine root biomass of the species.

Root adaptations

In addition to the climatic variables that strongly control shoot growth, roots and symbionts exist in an environment where the soil chemical and physical environment may significantly modify their growth dynamics. For example, while the shoot of a tree can be defined as an individual that is competing with other trees for light resources, this distinction is frequently not so clear belowground where fine roots of many plants intermingle extensively. For example, trees of many species are capable of root grafting with one another or with those of other species (Graham and Bormann 1966) or potentially have mycorrhizal hyphal connections between different plants (Ritz and Newman 1984; Finlay and Read 1986) so that the entire belowground part of a forest may have to be considered as one responding unit instead of many individuals forming a stand (Vogt et al. 1993). The importance of root grafting was observed in the 1960s when systemic chemicals were used to kill trees and many adjacent trees that were not treated also died because of the transfer of the chemical through root grafts (Bormann and Graham 1960). On the positive side, there is the potential that a plant may increase its ability to acquire nutrients limiting plant growth, or carbohydrate, if the plant is able to acquire these compounds from neighbours through root and/or mycelial connections (Finlay and Read 1986). These characteristics make it very difficult to compare the competitive environment of the shoot with that of the root at an individual plant level.

Plant roots are capable of modifying their morphology in response to edaphic conditions. One example relevant to wet tropical ecosystems, because of high precipitation rates, is the morphological adaptation of fine roots to high water levels. This adaptation is typically observed on stems and roots, where tissues are modified to contain internal gas spaces that function in transport and storage of oxygen in structures called aerenchyma, under conditions of low oxygen availability (Drew and Stolzy 1991; Waisel and Agami 1991). How common aerenchyma is in tropical systems is not known; its presence has been predominantly studied in areas with excess water (i.e. epiphytes in cloud forests with aerial roots, Benzing 1991). In secondary tropical forests in Puerto Rico, several tree species—even on ridge slopes, where water accumulated in small depressions after storms—have aerenchyma (Vogt unpublished). This adaptation is therefore relevant not only in riparian zones but in areas where soils may have a high clay content and surface water accumulates for short time periods.

Characteristics of mycorrhizal associations

Types and distribution of mycorrhizal associations

Two main types of mycorrhizal associations are relevant to plantation management: ectomycorrhizas and vesicular-arbuscular (VA) mycorrhizas. Less common mycorrhizas which will not be considered here include ericoid, arbutoid, monotropoid, orchid and E-strain (Harley and Smith 1983).

Ectomycorrhizal roots are characterised by a change in their morphology which causes an increase in the surface area of the root. The fungi expand the fine roots to an extensive network of short, multi-branched root systems which are larger in diameter than roots not colonised by fungi. Ectomycorrhizas can be recognised because of the distinct root branching pattern and the formation of an external mantle of fungal tissue which surrounds each root tip and can be quite colourful (ranging from white to purple to fluorescent green). In addition, ectomycorrhizas produce an internal hyphal network (the 'Hartig net') which separates cortical cells from one another and where nutrient exchange occurs between the fungus and the plant root.

Vesicular-arbuscular mycorrhizas do not structurally modify the root exterior and are primarily located inside root cortical cells. The distinguishing features of VA mycorrhizas are vesicles and arbuscules produced within root tissue. These can be observed only under a microscope after sectioning and staining root samples. These structures are believed to play a role in carbohydrate storage and phosphorus transfer.

In general, ectomycorrhizas are found in environments where the soils are low in nitrogen (N) or where N is sequestered in detrital material and unavailable to plants because of slow decay, while VA mycorrhizas are found colonising plants when phosphorus (P) availability is low (Harley and Smith 1983; Allen 1991). Furthermore, ectomycorrhizal fungi are commonly found in mesic climatic zones and where soil organic matter is abundant, while VA fungi are more common in arid and semi-arid climatic zones and where soils have low content of organic matter (Allen et al. 1995). However, both mycorrhizal types are frequently found on the same site since plant growth may be limited by insufficiency of both N and P.

Plant families which are ectomycorrhizal include Fagaceae, Dipterocarpaceae, Pinaceae, Myrtaceae, Salicaceae and Betulaceae, as well as a few species in Leguminosae, Rosaceae and Euphorbiaceae (Newman and Reddell 1987). VA mycorrhizas are more ubiquitous and are found in most non-ectomycorrhizal plants with the exception of rushes and sedges (Powell 1980; Allen 1991). VA mycorrhizas may also form dual or tripartite associations with ectomycorrhizas and/or nitrogen fixing plants in some trees such as *Alnus* and *Eucalyptus* (Trappe 1962; Chilvers et al. 1987; Allen 1991). Only about 1% of the total number of vascular plant species in the world have been surveyed for their mycorrhizal status (Newman and Reddell 1987), and only an estimated 5–10% of mycorrhizal fungal species have been described (Allen et al. 1995).

Mycorrhizal attributes

In a mycorrhizal association, the fungi increase uptake of nutrients by the plant and protect plant roots against soil pathogens, while the plant supplies the growth and maintenance requirements of the fungus by translocating assimilate to the fungus (Harley and Smith 1983). In cold temperate coniferous ecosystems, the presence of fungi increases the longevity of the root from several weeks to many years (Vogt and Bloomfield 1991). Clearly factors that reduce photosynthetic capacity of the plant will limit the ability of the plant to sustain this relationship. For example, shading a seedling stopped the development of fruiting bodies of mycorrhizal fungi associated with its roots (Harley and Smith 1983).

Many benefits, mainly identified in greenhouse and laboratory studies, have been attributed to the mycorrhizal association. It is important to test these benefits in the field if these associations are to be used in practical management. It has been hypothesised that mycorrhizal associations assist a plant to survive and grow by minimising the plant's exposure to toxic chemicals in the soil, increasing nutrient uptake under low soil nutrient availabilities and reducing mortality of root tissues due to pathogens in the soil (Vogt et al. 1991a). Mycorrhizae can be thought of as an interface between the plant and the soil environment that increases a plant's ability to occupy a site by ameliorating or filtering out negative factors in the soil that could reduce plant growth (Marx 1969, 1973; Harley and Smith 1983; Burgess and Malajczuk 1989; Vogt et al. 1991a).

Mycorrhizas are reported to have improved uptake of N, P and K by a range of plant species in greenhouse experiments (Fitter 1977; Alexander 1981; Hall et al. 1984; Bolan 1991). Enhanced uptake of N and/or P by ectomycorrhizas may be due to two mechanisms: 1) increasing the surface area of roots in a given unit of soil; and 2) solubilising P from poorly soluble sources in the soil by the production of phosphatases and utilising N from organic sources (Alexander 1981; Harley and Smith 1983; Bolan 1991). Outcomes from studies of potential enhancement of water relations by mycorrhizas have been inconclusive (Allen et al. 1981; Allen and Allen 1986). It is not clear if the increased uptake of water by mycorrhizal plants is a direct effect of the fungus or the fact that improved P nutrition indirectly affects plant water relations. Further research is needed to determine more definitively how mycorrhizas benefit the host plant under field conditions in the tropics and under what conditions these benefits are realised.

The ability of mycorrhizas to support plants to grow in environments with high and/or toxic levels of heavy metals has been shown in the field for cold and warm temperate conifers, and the mechanisms involved have been analysed (Allen and Allen 1980; Dahlgren et al. 1991; Wilkins 1991). Mycorrhizas can act as a selective membrane that reduces a plant root's exposure to toxic metals such as aluminium (Al) by decreasing the amount of Al that gets into the biologically active portions of plant tissues by selectively excluding or sequestering these metals in their own tissues (Danielson 1985; Vogt et al. 1987a,b, 1991a; Dahlgren et al. 1991; Wilkins 1991). Reclamation and restoration of minespoil and other disturbed lands can be assisted by inoculation of plants with mycorrhizal fungi (Daft and Hacskaylo 1976; Allen 1989; Miller and Jastrow 1992).

Variability in host plant and fungus relationships

Host plants display a high degree of variability in their 'mycorrhizal dependency', defined as their ability to grow without mycorrhizas. Plants range from obligate (high dependency) mycotrophs which are unable to survive without mycorrhizas, to facultative (low dependency) mycotrophs which can survive under some conditions without mycorrhizas, to non-mycorrhizal plants which do not generally form mycorrhizal associations (Janos 1980; Malloch et al. 1980). Obligately mycotrophic plants commonly grow in very stressed environments (i.e. low temperatures, low nutrient availability), facultative mycotrophic plants grow in low-stress environments while non-mycorrhizal plants are found under low-stress conditions where nutrient availability is high but disturbance frequent. The degree of dependency of a plant on mycorrhizas is relevant to the importance of managing mycorrhizas in plantations.

Experience with *Pinus caribaea* in the American tropics demonstrated that this tree was unable to grow in a healthy manner without mycorrhizas—seedlings were stunted and nutrient-deficient until they were inoculated with appropriate mycorrhizal species (Marks and Kozlowski 1973).

VA and ectomycorrhizal fungi have different capacity to improve plant growth and nutritional status, have different optimum soil fertility and pH ranges at which they are capable of maintaining the mycorrhizal association and have different temperature ranges at which they are able to survive and grow (Harley and Smith 1983; Hung and Trappe 1983; Abbott and Robson 1991; Allen 1991). Furthermore, within the mycorrhizal types, individual species of symbiotic fungi vary in their capacity to colonise different host plant species — there typically exists greater specificity between the plant and ectomycorrhizal fungi while VA fungi have less specificity and form associations with many different plant families (Trappe 1962; Harley and Smith 1983). It is only recently that new molecular techniques have allowed researchers to begin identifying mycorrhizal fungi to the species level in the field (Gardes et al. 1991), a valuable development. Certain isolates of mycorrhizas are more effective than others in improving plant growth and P or N uptake in glasshouse experiments (Marks and Kozlowski 1973; Alexander 1981; Harley and Smith 1983; Schubert and Hayman 1986; Allen 1991).

Tree productivity, carbon allocation and abiotic controls

Roots

Several studies on cold temperate conifers have shown decreased carbon allocation to fine roots when water and/or nutrient availability was increased (Keyes and Grier 1981; Kurz 1989; Vogt et al. 1990; Gower et al. 1992, 1994, 1997). In a *Pseudotsuga menziesii* forest in Washington, Keyes and Grier (1981) determined that at a high-quality site a 40-yr-old stand allocated 8% of its total net primary production to fine roots in contrast to a stand of similar age on a low-quality site that allocated 36% of its NPP to fine roots. Analogous allocation patterns to the Keyes and Grier (1981) study were obtained by Kurz (1989) for *P. menziesii* growing in British Columbia, Canada. Similarly, a montane *P. menziesii* forest in New Mexico allocated 34% less total NPP to fine roots when it was fertilised with N (Gower et al. 1992).

The pattern of increased allocation of carbon to roots with decreasing availability of nutrients found in temperate zones should be applicable to the tropics. Results of one tropical study in 5.6-yr-old *Eucalyptus grandis* plantations in the State of Sao Paulo, Brazil, (Goncalves 1994) do parallel those obtained for *P. menziesii*: sites with high productive capacity had low fine root biomass (1584 kg ha^{-1}) while sites with low productive capacity had high root biomass (2844 kg ha^{-1}).

What controls the amount of root biomass maintained, and its rate of turnover, is not clear when comparing different vegetation communities across climatic zones. For example, Nadelhoffer et al. (1985) hypothesised that in hardwood-dominated forests in Wisconsin fine root NPP should increase as the amount of N increased—opposite the pattern obtained for *P. menziesii*. They suggested that fine root biomass would be lower in nutrient-poor sites but that total allocation to maintaining fine root production would be higher because of a faster turnover of fine root tissues. Using mini-rhizotron technology in hardwood-dominated sites in Michigan, USA, however, Pregitzer et al. (1993) showed that with higher levels of nutrients and water root longevity was increased, rather than decreased as suggested by Nadelhoffer et al. (1985).

It is premature to generalise how water and nutrients change fine root NPP and turnover in forests. Many factors may influence the direction of these relationships, such as: 1) differences in individual tree species efficiency in resource (i.e., nutrients and water) acquisition from the soil and their use within the tree; 2) the ability of trees to utilise organic and inorganic forms of N (i.e., nitrate and ammonium); and 3) species differences in within-tree carbon allocation to above- and belowground biomass and secondary compounds. Field experimental manipulations of water and nutrients have been confounded by the difficulty of determining when nutrients and when water controls tree root growth. If water availability limits tree growth on a site, it may override the effect of a nutrient limitation (Gower et al. 1994). In the *P. menziesii* site in New Mexico where some stands were irrigated, others received N fertilizer applications and others were both irrigated and fertilised, both water and nutrients limited tree growth but at different times during the year (Gower et al. 1992). The limitation of water availability on root growth is difficult to separate from nutrient limitations since irrigation concurrently increases nutrient availability by speeding decomposition (Vogt et al. 1990).

The different relationship reported between N and fine root growth for *P. menziesii* and the hardwood sites in Wisconsin may be partially explained by what is the dominant inorganic N form in the soil. For example, *P. menziesii* sites have N available in the ammonium form (Vogt 1987) while the sites in Wisconsin had a high nitrate-N availability (Nadelhoffer et al. 1985). It has been shown that nitrate nitrogen changes root development by resulting in roots with less branching and fewer fine root tips (Vogt et al. 1990). A field study of (manipulated) forms of inorganic N is necessary to determine how they affect root growth and maintenance costs.

In the tropical pine and mahogany plantations and secondary forests studied by Lugo (1992) in Puerto Rico, differences in carbon allocation to above and belowground biomass were reported for trees of the same age but different species growing adjacent to one another. While both plantations and secondary forests achieved similar total NPP, there were significant differences in how much carbon was allocated to above and belowground biomass. A summary of the studies conducted in the tropics (Table 8.1) does show a general pattern of lower (4–11%) total living biomass allocated to roots in plantations compared to natural forests (6–33%). However, these differences are not distinctive characteristics of plantations compared to secondary forests but are attributes of the species grown in the plantations (Lugo 1992; Vogt et al. 1995b). The impact of different carbon allocation patterns by species on ecosystem-level carbon and nutrient cycling needs to be examined. If trees in plantations allocate less carbon to fine root mass and associated mycorrhizas, will it affect their susceptibility to insects and pests, and their ability to recover after disturbance?

Symbiotic associations

Ectomycorrhizal and VA mycorrhizal associations require different amounts of assimilate from the host plant to maintain the relationship. Ectomycorrhizas, with their greater biomasses and more extensive sheath and hyphal networks, require a greater carbohydrate investment by the host plant than do VA mycorrhizas.

Field studies that estimated the cost to the plant of maintaining ectomycorrhizal associations have been conducted in the temperate forests, but the findings are underestimates since not all contributions of symbionts to the carbon cycle were included. For example, Rommell (1939) estimated that 10% of the potential timber production in a spruce *(Picea abies* L. Karst.) forest was used to produce ectomycorrhizal sporocarps. In a study of an *A. amabilis* ecosystem by Vogt et al. (1982), 15% of the total net primary production was allocated to the ectomycorrhizal fungal symbiont (including sporocarps, fungal sheaths and Hartig nets). Neither study included respiratory carbon losses or losses of carbon as exudates from ectomycorrhizas (Vogt et al. 1991a). Although losses of carbon dioxide from mycorrhizal roots as a proportion of total carbon fixed by a plant have not been measured in the field, laboratory and greenhouse estimates range from 10 to 30% Harley and Smith 1983; Reid et al. 1983; Rygiewicz and Andersen 1994).

As well as the carbon cost, mycorrhizal associations modify the physiology of the plant and change the rate at which carbon is cycled within the plant. Using *P. menziesii* seedlings growing in controlled conditions, Rygiewicz and Andersen (1994) showed that even though only 5% of the total seedling dry weight was in fungal tissue the presence of the symbionts increased carbon allocation belowground by 23% compared to non-mycorrhizal plants. In this study, the mycorrhizal plants accumulated less total biomass compared to non-mycorrhizal plants since carbon was being allocated to the development of the mycorrhizal association and the hyphal network extending from the roots. Reid et al. (1983) reported that *Pinus taeda* inoculated with mycorrhizal fungi assimilated more $^{14}CO_2$, allocated a greater percentage of assimilated ^{14}C to root systems, and lost a greater percentage of ^{14}C by root respiration than did non-mycorrhizal plants. Allen et al. (1981) reported a 68% increase in the photosynthetic rate of mycorrhizal compared to non-mycorrhizal plants.

Stand development and succession

Fine roots

Several studies have examined the development of fine root biomass along successional sequences in temperate forests (Gholz et al. 1986; Vogt 1987; Vogt et al. 1987c). These studies generally show fine root biomass peaking at canopy closure and levelling off after this time (Vogt et al. 1987c). The main effect of nutrient availability on this relationship was that a *P. menziesii* stand at a lower quality site reached canopy closure after 40 yr of age while a higher site quality stand reached canopy closure 10–15 yr earlier (Vogt et al. 1987c). Even though the fine root biomass may not increase with increasing stand age, a greater proportion of total carbon fixed by a plant appears to be allocated to roots. For example, in subalpine *Abies amabilis* stands, 36% of total NPP was allocated to fine roots (<2 mm) in a 23-yr-old stand, but this fraction increased to 66% by 180 yr (Vogt et al. 1982).

The relative importance of root biomass and surface area in the different root diameter classes will vary with the developmental stage of the plant (Vogt et al. 1989). During the first year of seedling growth most of the roots are in the fine root category, in contrast to mature trees that may have <5% of total roots in this category. For example, a 30-yr-old *A. amabilis* tree with a stem diameter of 2.0 cm at 15 cm stem height had 14% of total root weight and 56% of the total surface area in the <2 mm root diameter class, while a plant with a stem diameter of 6.5 cm at 15 cm stem height had 4% of the total root weight and 15% of the total root surface area in the <2 mm class (Vogt et al. 1989).

Symbiotic associations

Successional changes in mycorrhizal fungi within the same ecosystem have been observed in both relatively undisturbed forests (Schenck et al. 1989; Vogt et al. 1981, 1992) and plantations in the temperate zone (Chilvers et al. 1987; Termorshulzen and Schaffers 1989; Richter and Bruhn 1993). In *Eucalyptus* plantations (a genus capable of forming concurrent associations with VA and ectomycorrhizal fungi), mycorrhizal colonisation progresses from a VA-dominated system during early stages of plantation growth to ectomycorrhizal fungi in later stages (Lapeyrie and Chilvers 1985; Chilvers et al. 1987; Mendonca Bellei et al. 1992). Pine species also show successional change in mycorrhizal colonisation of root tips, generally having an increase in species richness and abundance of colonised root tips with increasing tree age following transplanting to the field (Chu-Chou 1979; Chu-Chou and Grace 1982, 1987, 1988; Richter and Bruhn 1993). However, in another study comparing young (5–13 yr) and older (50–80 yr) plantations, Termorshulzen and Schaffers (1989) observed that the number of mycorrhizal species was greatest for the younger trees and the number of unique species (i.e., not occurring on other stands) was also greatest during the early stages of plant growth. Such successional change in the mycorrhizal species on roots needs to be considered in understanding how propagules of different fungal species are able to reach plantations at different stand ages.

Management activities that affect surface organic horizons or the soil may influence mycorrhizal fungal succession. For example, *Coriaria* (Coriariaceae) will have ectomycorrhizas, VA fungi and *Frankia* nodules on the same root system when growing in a pine-oak forest but it loses the ectomycorrhizal associations when the soil is disturbed (Cruz-Cisneros and Valdės 1990). *Eucalyptus marginata* will form symbiotic associations with VA fungi when the roots are located in the mineral soil but roots restricted to the surface organic horizons have only ectomycorrhizal associations (Reddell and Malajczuk 1984).

We know from laboratory and greenhouse studies that many symbionts are capable of colonising one tree species (Trappe 1962; Brundrett 1991) but we do not have a good understanding of what determines the diversity found in the field. For example, Trappe (1962) noted that over 2000 different species of fungi were capable of forming a symbiotic relationship with one tree species while field measurements typically recorded only 7 species of symbionts in a mature forest (Vogt et al. 1981). It is not clear how many different species can be maintained on the root system of a tree growing in a plantation, what level of diversity is desirable or what the effects of management activities are on species diversity. Despite this, researchers have attempted to increase the diversity of mycorrhizas in plantations. For example, Ikram et al. (1992) introduced a high-diversity inoculum of VA mycorrhizas (eight VA species) for rubber *(Hevea brasiliensis)* seedlings in Malaysia. There appears to be some limitation on how many different species will be found on the root systems of trees in forests. For example, a study in pine plantations in Sweden showed that the original composition of mycorrhizas introduced 13 yr earlier had been totally replaced even though the degree of colonisation was undiminished (Arnebrant et al. 1990). Since different nutrients are unevenly distributed in the soil, the existence of diverse mycorrhizal fungi on tree roots may assist a plant to effectively access this heterogeneous resource.

Nutrient cycling, roots and mycorrhizal associations

Fine roots and mycorrhizas have an important role in modifying the cycling of nutrients in ecosystems because they: 1) contribute to nutrient uptake; 2) change the rate at which nutrients and heavy metals are recycled and stored; and 3) contribute significantly to nutrient cycling rates when they die and decompose (Vogt et al. 1986; Vogt et al. 1991b; Bloomfield et al. 1993). These are discussed further below.

Nutrients and plant carbon allocation

Nitrogen has a significant effect on plant carbon allocation patterns in temperate zone forest ecosystems. Nitrogen uptake from the soil influences the source-sink relationships of photosynthetically-fixed carbon in trees in temperate forests (Waring and Schlesinger 1985; Lechowicz 1987; Vogt et al. 1987b). Its effects on tree growth and carbon allocation in tropical plantations have yet to be determined. In addition to N, it is also important to understand the effects of K, Ca and P fertilisation on trees in the tropics because deficiencies of these nutrients limit growth of tropical trees (Wadsworth 1983; Jorgensen and Wells 1986). How scarcity of these nutrients might affect carbon allocation patterns in trees needs to be determined. In temperate zones, nitrogen fertilisation and/or irrigation (which increases the availability of N in the soil) of forests increased carbon allocation to coarse roots but decreased that allocated to fine roots, thus effectively decreasing the nutrient- and moisture-acquiring area of the plants (Vogt et al. 1990; Gower et al. 1992).

In general, as N availability increases, plants decrease carbon allocation (as a proportion of the total carbon fixed) to root biomass, to mycorrhizal fungi and to secondary defensive chemicals, and increase allocation to aboveground tissues (foliage and stems) (Waring et al. 1985). Decreases in fine root and mycorrhizal biomass due to excessive addition of one nutrient with strong effects on carbon allocation can result in deficiencies in other nutrients (Vogt et al. 1990). The negative consequences of excessive nutrient additions have been shown in several experimental studies in forests in Sweden (Persson 1980; Axelsson 1984). The shift in carbon allocation to the aboveground from belowground biomass in plantations has to be analysed from the perspective that roots have a role in maintaining tree health by increasing nutrient uptake by plants under conditions of low decomposition rates (Vogt et al. 1986; Vogt et al. 1991b), that they are a supporting mechanism for avoiding Al toxicity (Vogt et al. 1987b) and that the starch stored in them can be utilised to prevent fungal pathogens entering the plant (Wargo 1972).

Recently there has been interest in developing total nutrient cycling budgets (which include above- and belowground biomass plus soils data) for tree plantations and secondary or primary forests to assess the potential impact of fast-growing tree species on soil nutrient levels and long-term sustainability of plantations (Table 8.3;

Russell 1987; Cuevas et al. 1991; Montagnini et al. 1991; Lugo 1992). These budgets show that plantations maintain a smaller fraction of the total N in the living biomass in roots (typically <15%), while natural forests store a larger fraction of their N in roots (17–35%, Table 8.3). Similarly plantations had less than 10% of total P in living roots while natural forests had 11–41% in roots (Table 8.3). Somewhat similar patterns occurred for K but the differences between forests and plantations were not as large (Table 8.3). A greater proportion of nutrients in living biomass are potentially removed during harvesting in plantations than in natural forests. The soil reserves of all three nutrients, however, were quite high in the cases reported in Table 8.3, suggesting a high capacity of the soil to replenish nutrients removed during harvesting.

Roots, mycorrhizas and nutrient availability

Fine roots and mycorrhizas may affect soil nutrient availability through the secretion of organic acids, soluble sugars and carbon dioxide produced from respiration (Johnson et al. 1977; Schwab et al. 1983), and upon senescence of fine root and mycorrhizal tissues. In two subalpine *A. amabilis* stands in Washington, USA, an estimated 15% of the total organic material returned to the soil was derived from mycorrhizal tissues despite the fact that they accounted for less than 3% of the total living biomass (Vogt et al. 1982). Furthermore, in a *P. menziesii* stand in Oregon, USA, mycorrhizal roots comprised an estimated 6% of the living biomass while contributing 48% of the organic matter to the soil (Fogel and Hunt 1983). These inputs by mycorrhizal fungi consist of tissues that have high nutrient contents and should decay rapidly.

Decomposing fine roots may also increase the nutrient storage capacity of tropical forests. In secondary tropical forests in Puerto Rico, fine roots decayed and released minerals at a slower rate than foliage in the same site (Bloomfield et al. 1993). This means that dead roots potentially act as a longer-term store for nutrients and may be important in minimising nutrient losses. Questions related to the role of roots and mycorrhizas in nutrient cycling and conservation are critical areas needing research since many tropical plantations are located on nutrient-poor soils and some of the failures of tropical plantations have been attributed to low nutrient availability (Fearnside and Rankin 1985; Moran 1986; Lugo et al. 1990).

Mycorrhizas also directly respond to microsites of higher nutrient availability in the soil. The length of VA mycorrhizal hyphae involved in nutrient transport increased with decreasing organic matter content and total soil mineral content (McNaughton and Oesterheld 1990). Fine roots and mycorrhizal hyphae have also been shown to concentrate in areas of high organic matter content (St John et al. 1983). By contributing directly to carbon and nutrient stores in the soil and by selectively exploiting pockets of high nutrient availability, fine roots and mycorrhizal fungi affect the cycling of these materials within the system.

Results from laboratory and greenhouse studies suggests that trees may transfer metabolites and nutrients through belowground connections to neighbouring individuals via intra- and inter-specific mycorrhizal hyphal connections or through root grafts (Brownlee et al. 1983; Read et al. 1985; Newman 1988). Under more controlled conditions, Newman and Eason (1989) reported that ^{32}P was transferred from dying to living roots of two VA mycorrhizal plants *(Lollium perenne–L. perenne* and *L. perenne–Plantago lanceolata)* but not between a mycorrhizal and a non-mycorrhizal plant *(Lollium perenne–Brassica oleracea)*. More experiments are needed to determine whether the amount of nutrients transferred is large enough to play a significant role in nutrient cycling processes and the potential for managing for mycorrhizal hyphal interactions in plantations.

Because of the role mycorrhizas play in P uptake, the degree of mycorrhizal colonisation of root systems has been shown to be inversely related to soil P concentrations (Johnson et al. 1991). Therefore P fertilisation may have direct effects on mycorrhizal associations. Similarly N fertilisation produces a fast-growing root that eliminates the symbiont from the root. Studies on effects of fertilizer on plantation performance rarely consider the implications for the symbiont component under field conditions. A study by Johnson (1993) of VA mycorrhizal communities in fertilised and unfertilised agricultural fields in Minnesota found that fertilisation altered the species composition of the mycorrhizae, resulting in dominance of mycorrhizal species which had lower effectiveness in improving plant performance. The fungi from the fertilised soil produced fewer hyphae and arbuscules and the same number of vesicles as fungi from unfertilised soil, and were therefore considered to be 'inferior mutualists' (Johnson 1993).

Theoretically it should be possible to determine what level of P fertilisation is optimal for enhancing plantation crop production while minimising the suppression of the mycorrhizal association, but this will require field experiments which monitor mycorrhizal–plant interactions at various levels of P fertilisation. This would also depend on tree species differences and the diversity of symbionts located on the root systems. Laboratory and greenhouse experiments have found differences in tree species responses to fertilizer with and without mycorrhizas. For example, Browning and Whitney (1992) found that inoculated *Picea mariana* seedlings had significantly greater dry weight biomass (44%) than uninoculated controls at low soil P levels, while inoculated *Pinus banksiana* seedlings had greater dry weight biomass than uninoculated seedlings at both high and low levels of soil P (26% and 33%, respectively). These results suggested that *P. banksiana* may tolerate higher levels of P fertilisation if mycorrhizal colonisation can be maintained by inoculation, while inoculation of *P. mariana* will be beneficial only under low P applications. Conversely, another approach would be to select for strains of mycorrhizas that are more effective at the soil P levels desired with the fertilisation regime. Schubert and

Hayman (1986) demonstrated that different VA mycorrhizal species varied in their capacity to improve plant growth under different levels of soil P, suggesting that selection of field inoculants may be made based on mycorrhizal behaviour under conditions of elevated soil P. The applicability of these observations under field conditions, however, is not yet clear.

Most studies on mycorrhizae focus on P (Table 8.4). This ignores the fact that other abiotic variables may be limiting plant growth or that soil chemical attributes may be having a stronger influence on modifying P availability in the field. For example, P may be strongly controlled by Al cycling in the soil (Dahlgren et al. 1991), which means that the forms of Al in the soil may determine what levels of P the plants plus associated mycorrhizas will have access to. Since potential Al toxicity is considered to exist over 60% of the soils in the tropics (Moran 1986), it is important to also examine the role of Al in affecting P availability.

Pot experiments have suggested that mycorrhizas may enhance heavy metal tolerance in the host plant (Brown and Wilkins 1985; Wilkinson and Dickinson 1995) but this characteristic varies by both fungal and plant species and cannot be generalised. The differential tolerance of plants to heavy metals may be strongly driven by which symbionts are on the root systems, how well developed are the relationships between plant and fungus, and also whether the plant is a metal accumulator. For example, in an ecosystem in Washington state, USA, *A. amabilis* had well developed mycorrhizas which appeared to reduce the uptake of Al at the root level. The associated tree species *(Tsuga mertensiana*, an Al accumulator) had the same symbionts on its root systems but the mutualism was poorly developed between the fungus and root and the trees accumulated high levels of Al in their leaves (Vogt et al. 1987a).

Table 8.1. Total and root biomass of tropical and subtropical forests and plantations

Species	Root sampling frequency	Stand age (yr)	Above- and belowground living biomass (t ha^{-1})	Biomass of fine or small roots (t ha^{-1})	Fraction of total living biomass in total roots (%)	Source
Plantations						
Theobroma cacao + *Cordia alliodora*	1	5	45.9[a]	4.2[b]	9	Alpizar et al. 1986, Fassbender et al. 1991
Theobroma cacao + *Cordia alliodora*	1	10	95.4[a]	9.8[b]	10	Alpizar et al. 1986, Fassbender et al. 1991
Pinus caribaea	1	4	40.8	1.6[b]	7	Lugo 1992
P. caribaea	4	11	95.6[a]	0.7[b]	–	Cuevas et al. 1991
P. caribaea	1	18.5	186.0	4.6[b]	11	Lugo 1992
Swietenia macrophylla	1	17	102.0	3.0[c]	8	Lugo 1992
S. macrophylla	1	49	127.0	3.2[c]	4	Lugo 1992
Stryphnodendron microstachyum	1	4	54.9[a]	5.5[i]	10	Montagnini et al. 1991, 1994
Vochysia guatemalensis	1	4	55.5[a]	2.8[i]	5	Montagnini et al. 1991, 1994
V. ferruginea	1	4	49.9[a]	4.9[i]	11	Montagnini et al. 1991, 1994
Hyeronima alchorneoides	1	4	43.9[a]	4.6[i]	11	Montagnini et al. 1991, 1994
Jacaranda copaia	1	3[a]	50.1[a]	1.3[g]	3	McGroddy 1994, Montagnini et al. 1995
Vochysia guatemalensis	1	3	28.4[a]	2.3[g]	8	McGroddy 1994, Montagnini et al. 1995
Mixed plantation	1	3[a]	33.6[a]	1.1[g]	3	McGroddy 1994, Montagnini et al. 1995

Table 8.1. (cont'd) Total and root biomass of tropical and subtropical forests and plantations

Species	Root sampling frequency	Stand age (yr)	Above- and belowground living biomass (t ha^{-1})	Biomass of fine or small roots (t ha^{-1})	Fraction of total living biomass in total roots (%)	Source
Natural forests						
Bana	1	Mature	92.0^a	16.2^f	–	Sanford 1989
Caatinga	1	Mature	246.0^a	18.7^f	–	Sanford 1989
Tierra firme	1	Mature	396.0^a	14.3^f	–	Sanford 1989
Tierra firme	1	11	61.0^d	n.d.	13	Saldarriaga et al. 1988
Tierra firme	1	20	73.0^d	n.d.	16	Saldarriaga et al. 1988
Tierra firme	1	35	130.0^d	n.d.	16	Saldarriaga et al. 1988
Tierra firme	1	60	244.0^d	n.d.	19	Saldarriaga et al. 1988
Tierra firme	1	80	170.0^d	n.d.	16	Saldarriaga et al. 1988
Tierra firme	1	Mature	268.0^d	n.d.	17	Saldarriaga et al. 1988
Primary forest	5	Mature	178.0^a	7.4^h	–	Priess and Folster 1994
Secondary forest	5	Young	79.0^a	11.4^h	–	Priess and Folster 1994
Secondary forest	5	50	190.0^a	10.3^h	–	Priess and Folster 1994
Secondary forest	4	Mature	23.0^a	5.3^c	–	Cuevas et al. 1991
Dry forest	12		28.0^a	1.6^c	–	Singh and Singh 1991
Secondary forest — evergreen	1	4	33.0	4.5^c	33	Lugo 1992
Secondary forest — evergreen	1	17	81.0	5.4^c	16	Lugo 1992
Secondary forest— evergreen	1	18.5	111.0	4.9^c	19	Lugo 1992
Secondary forest — evergreen	1	49	99.0	4.3^c	21	Lugo 1992
Secondary forest — evergreen	1	Mature	302.0^j	8.2^d	27	Scatena et al. 1993, Kangas 1992

Table 8.1. (cont'd) Total and root biomass of tropical and subtropical forests and plantations

Species	Root sampling frequency	Stand age (yr)	Above- and belowground living biomass (t ha^{-1})	Biomass of fine or small roots (t ha^{-1})	Fraction of total living biomass in total roots (%)	Source
Pinus massoniana	1	30	92.0[a]	9.3[fc]	10	Mo et al. 1995
Secondary forest	1	2	2.0[d]	n.d.	10–22	Ewel 1971
Secondary forest	1	4	4.0[d]	n.d.	6–7	Ewel 1971
Secondary forest	1	6	5–7[d]	n.d.	25–26	Ewel 1971
Broadleaf semi-deciduous	1	50	359.0[d]	n.d.	15	Vogt et al. 1995a
Secondary forest	1	16	237.0[d]	n.d.	14	Vogt et al. 1995a
Secondary forest	1	10	n.d.[a]	15.9[gd]	–	McGroddy 1994
Secondary forest	1		n.d.[a]	7.9[id]	–	Montagnini et al. 1991

[a]Does not include coarse structural roots; [b]fine roots classified = <5 mm–20 mm; [c]fine roots equal to or less than 2 mm; [d]coarse roots only; [e]fine roots < 5 mm; [f]roots sampled to 10 cm soil depth; [g]roots sampled to 15 cm depth; [h]roots sampled to 20 cm depth; [i]roots sampled to 60 cm depth. [j]used fine root data <5 mm (8.2 t ha^{-1}) from Kangas (1992) instead of Scatena et al. 1993 (2.2 t ha^{-1}) since that reported in the latter article was hurricane impacted and too low for an undisturbed forest

Table 8.2 Above- and belowground net primary production of tropical forests and plantations

Species	Age (yr)	Aboveground NPP (t ha^{-1} yr^{-1})	Belowground NPP (t ha^{-1} yr^{-1})	Total NPP (t ha^{-1} yr^{-1})	Source
Plantation					
Pinus caribaea	4	7.9	–	–	Lugo 1992
Pinus caribaea	11	18.1	1.1	19.2	Cuevas et al. 1991
Pinus caribaea	18.5	15.1	–	–	Lugo 1992
Swietenia macrophylla	17	16.6	–	–	Lugo 1992
Swietenia macrophylla	49	19.1	–	–	Lugo 1992
Theobroma cacao + *Cordia alliodora*	5–10	22.7	5.5	28.2	Fassbender et al. 1991
Natural forest					
Secondary	4	7.9	–	–	Lugo 1992
Secondary	11	11.0	8.5	19.4	Lugo 1992
Secondary	17	8.5	–	–	Lugo 1992
Secondary	18.5	10.0	–	–	Lugo 1992
Secondary	49	12.3	–	–	Lugo 1992
Primary	Mature	3.8	3.7	7.5	Priess and Folster 1994
Secondary	Young	2.7	5.7	8.4	Priess and Folster 1994
Secondary	50	2.6	5.2	7.8	Priess and Folster 1994

Table 8.3 Nitrogen, phosphorus and potassium storage in roots compared to the remaining living biomass and in relationship to soil content of these nutrients in plantations and naturally regenerating forests

Species	Age (yr)	Nitrogen		Phosphorus		Potassium		Source
		Total living tree N (kg ha^{-1}) (% of total living tree N in roots)	**Soil N (kg ha^{-1}) (% of total ecosystem N in the soil)**	**Total living tree P (kg ha^{-1}) (% of total living tree P in roots)**	**Soil P (kg ha^{-1}) (% of total ecosystem P in the soil)**	**Total living tree K (kg ha^{-1}) (% of total living tree K in roots)**	**Soil K (kg ha^{-1}) (% of total ecosystem K in the soil)**	
Plantation								
Pinus caribaea	4	359 (4)	8920 (96)	12.4 (7)	1710 (99)	50(22)	31480 (>99)	Lugo 1992
P. caribaea	18.5	1443 (5)	11630 (89)	54.8 (7)	1690 (97)	509 (13)	26250 (98)	Lugo 1992
Swietenia macrophylla	17	560 (8)	8110 (94)	28.5 (9)	1350 (98)	361 (7)	30010 (99)	Lugo 1992
S. macrophylla	49	998 (4)	5480 (85)	37.1 (10)	1410 (97)	412 (3)	18120 (98)	Lugo 1992
Theobroma cacao + *Cordia alliodora*	5	370 (10)[a]	7991 (96)	45.4 (9)[a]	3594 (99)	364 (6)[a]	577 (61)	Alpizar et al. 1986
Stryphnodendron microstachyum	4	467 (11)[a]	12925 (96)	37 (33)[a]	–	79 (10)[a]		Montagnini and Sancho 1994, Montagnini 1995
Vochysia guatemalensis	4	263 (10)[a]	13958 (98)	43 (13)[a]	–	177 (1)[a]		Montagnini and Sancho 1994, Montagnini 1995
Vochysia ferruginea	4	223 (20)[a]	13578 (98)	35 (36)[a]	–	77 (26)[a]		Montagnini and Sancho 1994, Montagnini 1995
Hyeronima alchorneoides	4	294 (15)[a]	11520 (97)	55 (14)[a]	–	256 (2)[a]		Montagnini and Sancho 1994, Montagnini 1995
Eucalyptus grandis	25	1117 (15)	3682 (77)	–	–			Drechsel and Zech 1992

Table 8.3 (cont'd) Nitrogen, phosphorus and potassium storage in roots compared to the remaining living biomass and in relationship to soil content of these nutrients in plantations and naturally regenerating forests

Species	Age (yr)	Nitrogen		Phosphorus		Potassium		Source
		Total living tree N (kg ha^{-1}) (% of total living tree N in roots)	Soil N (kg ha^{-1}) (% of total ecosystem N in the soil)	Total living tree P (kg ha^{-1}) (% of total living tree P in roots)	Soil P (kg ha^{-1}) (% of total ecosystem P in the soil)	Total living tree K (kg ha^{-1}) (% of total living tree K in roots)	Soil K (kg ha^{-1}) (% of total ecosystem K in the soil)	
Natural forests								
Secondary forest	4	218 (25)	5180 (96)	7.2 (41)	970 (99)	160 (36)	25040 (99)	Lugo 1992
Secondary forest	17	495 (24)	8440 (95)	35.9 (24)	2780 (99)	466 (13)	18720 (98)	Lugo 1992
Secondary forest	18.5	610 (17)	8020 (93)	34.4 (11)	1190 (97)	479 (12)	26990 (98)	Lugo 1992
Secondary forest	49	478 (21)	8880 (95)	29 (13)	2230 (99)	367 (9)	21090 (98)	Lugo 1992
Secondary forest	Mature	946 (35)[b]	7522 (89)	49 (32)[b]	–	602 (15)[b]		Scatena et al. 1993; Kangas 1992
Secondary forest	16	820 (17)	5500 (87)	–	–			Vogt et al. 1995
Pinus massoniana	30	219 (32)	–	11.5(39)	–	80 (40)		Mo et al. 1995

Note: See Table 8.1 for diameter size and depth of sampling for roots; [a]Does not include coarse roots; [b]Adjusted fine root data < 5 mm using Kangas's (1992) biomass of 8.2 t ha^{-1} instead using the 2.2 t ha^{-1} reported in Scatena et al. 1993 since this value reflected a hurricane-impacted number.

Table 8.4 Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
				Mycorrhizas—inoculation				
Theobroma cacao	Native	*Scutellospora calospora* *Glomus mosseae*	Sabah, Malaysia	3–6 months	Pot experiment	6 months	Improved growth and nutrient uptake of vegetative propagules with VAM[a] inoculation; inoculated VAM more effective than indigenous soil mycorrhizae.	Azizah Chulan and Martin 1992
Oil palm	n/a +	n/a	Ivory Coast	5 months	Pot experiment	5 months	Improved growth and nutrient uptake with inoculation by indigenous species. Effectiveness varied with mycorrhizal species.	Blal and Gianinazzi–Pearson 1989
Eucalyptus globulus	Native	*Laccaria laccata* *Scleroderma verrucosum* *Setchelliogaster* sp.	Australia	5 months	Pot experiment	5 months	Improved growth with inoculation; mycorrhizas reduced phenotypic variability of seedlings.	Burgess and Malajczuk 1989
Eucalyptus urophylla × *E. kirtoniana*	Exotic	*Pisolithus tinctorius* *Scleroderma texense* *S. dictyosporum* *S. aurantium* *S. cylindrosporum*	Congo	50 months	Plantation	50 months	Inoculation with exotic EM[b] improved growth but mycorrhizas varied in sustainability of effect and competed poorly with native mycorrhizas over long term.	Garbaye et al. 1988.
Acacia nilotica *Leucaena leucocephala*	n/a Exotic	*Glomus etunicatum* *G. mossae* *G. occultum*	Somalia	3 months	Pot experiment	3 months	Improved growth with indigenous VAM inoculation. Improved drought resistance of *L. leucocephala*, no change for *A. nilotica*.	Michelsen and Rosendahl 1990

Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Pinus caribaea *Pinus oocarpa*	Exotic	*Pisolithus tinctorius*	Nigeria	0–3 yr	Experimental plantation	3 yr	Successful survival of exotic mycorrhiza, *P.tinctorius* compared to indigenous soil inoculant. Improved growth and survival with inoculation.	Momoh and Gbadegesin 1980
P. caribaea	Exotic	*Pisolithus tinctorius* *Rhizopogon luteolus* *Thelephora terrestris*	Kumasi and Takoradi, Ghana	1 yr	Nursery	1 yr	Growth and survival varied with exotic inoculant species.	Ofosu-Asiedu 1980
Citrus volkameriana	n/a	*Glomus intraradices*	Florida, USA	3 months	Pot experiment	3 months	Analysis of carbon costs: growth depression in mycorrhizal citrus at high P^c supply.	Peng et al. 1993
Casuarina obesa	Exotic	*Glomus fasciculatum*	Lucknow, India	3 months	Greenhouse	3 months	Improved growth in alkaline soil with inoculation by indigenous mycorrhizas. Reduced root/shoot ratio in mycorrhizal seedlings.	Sidhu and Behl 1992
Pinus michoacana *Pinus pseudostrobus*	Native	*Pisolithus tinctorius* *Laccaria laccata*	Tepetlaoxtoc, Mexico	18 months–3 yr	Experimental plantation	3 yr	Improved growth and survival with inoculation; higher survival with *P.tinctorius* inoculant, higher mycorrhizal colonisation of *P. pseudostrobus*.	Valdés 1986

Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Hevea brasiliensis	Exotic	*Glomus* spp. *Sclerocytis* spp. *Acaulospora* spp. *Gigaspora* spp.	Sri Lanka	1–5 yr	Industrial plantation	n/a	Improved P uptake with mycorrhizal infection. No effect of mycorrhizas on *Hevea*'s growth. Greater mycorrhizal infection under legume ground cover; stimulation of nitrogen fixing activity by mycorrhizas.	Waidyanatha 1980
			Mycorrhizas — presence documentation studies					
Stryphnodendron microstachium	Native	n/a	La Selva, C.Rica	20 yr	Pot experiment	160 days	VAM inoculum potential of three vegetation types in abandoned pasture; seedling establishment.	Asbjornsen, and Montagnini 1994
Pinus radiata	Exotic	*Scleroderma* spp. *Endogone flammicorona* *Amanita muscaria* *Tuber* spp. *Rhizopogon rubescens* *Suillus* spp. *Hebeloma crustuliniforme* *Laccaria laccata* *Thelephora terrestris*	New Zealand	2–17 yr	Plantation and nursery	5 yr	Mycorrhizal diversity varied with forest and soil type. Greater diversity in older forests.	Chu-Chou and Grace 1988
Psuedotsuga menziesii	Exotic	*Hebeloma crustuliniforme* *Laccaria laccata* *Rhizopogon parksii* *Suillus lakei*	South Island, New Zealand	2–40 yr	Nursery and forest	6 yr	Different mycorrhizal associations in forests of different ages.	Chu-Chou and Grace 1987

Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Eucalyptus spp.	Exotic	*Hydnangium carneum* and others	North Island, New Zealand	Seedling –50 yr	Plantation	2 yr	Different mycorrhizal associations in forests of different ages.	Chu-Chou and Grace 1982
Coffee arabica	Exotic	n/a	Miranda State, Venezuela	25 yr	Industrial plantation	1 yr	High VAM infection of coffee roots; study of root biomass distribution, seasonal fine root growth, and litter decomposition. VAM infection did not affect decomposition rate of litter.	Cuenca et al. 1983
Shorea bracteolata *S. leprosula* *S. curtisii*	Native	n/a	Forest Research Institute of Malaysia, Kepong	n/a	Plantation and logged forest	1 month	High mycorrhizal infection of seedlings in 61-yr-old plantation and logged forest. Suggest that mycorrhizas have positive effect on P uptake.	Lee and Lim 1989
Citrus aurantifolia	n/a	n/a	Colima, Mexico	6–7 yr	Plantation and family garden	6 months	Indigenous VAM colonisation of plants was lower in high-input (irrigation, fertilised) agroecosystems vs. low-input systems.	Michel-Rosales and Valdés (in press)

Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Acacia spp. *Callistemon lanceolatus* *Casuarina equisetifolia* *Chamiaecytisus* sp. *Cordia africana* *Croton macrostachys* *Cupressus* spp. *Eucalyptus* spp. *Euphorbia pulcherrima* *Grevillea robusta* *Juniperus procera* *Leucaena leucocephala* *Olea africana* *Pinus patula*	11 native, 30 exotic, (not all species listed)	n/a	Somalia, Ethiopa	2–14 months	Nursery	4 yr	Mycorrhizal and root nodulation documented in tree seedlings. Degree of mycorrhizal colonisation varied by tree species.	Michelsen 1992
Cocos nucifera	n/a	n/a	Kasaragod, Kerala	25–30 yr	Experimental plantation	n/a	Reduced VAM on root (wilt) diseased plants. Higher VAM in intercropped system.	Thomas 1988
Mycorrhizas—fertilisation								
Hevea brasiliensis	Exotic	*Glomus manihot* *Glomus clarum* *Entrophospora colombiana* *Glomus macrocarpum* *Scutellispora calospora* *Glomus intraradix*	Kota Tinggi, Malaysia	26 weeks	Experimental plantation	26 weeks	Multi-species inoculant of indigenous VAM species used on seedling rootstock. Fertilisation with P decreased mycorrhizal root colonisation. Improved growth and nutrient uptake with inoculation when P limiting.	Ikram et al. 1992

Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Alnus nepalensis	Native	*Glomus mosseae*	Sillong, India	6 months	Pot experiment	6 months	Fertilisation w/P reduced VAM infection. Improved growth with inoculation when P limiting. VAM infection of N-fixing *Alnus* increased with successful nodulation and vice versa.	Jha et al. 1993
			Mycorrhizas—pesticides/herbicides					
In-vitro only	n/a	*Cenococcum geophilum* *Corticium bicolor* *Laccaria laccata* *Pisolithus tinctorius*	Dehra Dun, India	6 weeks	Lab experiment/ flasks	12 weeks	Inhibition of EM by 4 different pesticides.	Thapar and Uniyal 1990
Pinus radiata	Exotic	n/a	Victoria, Australia	3 and 6 months	Pot experiment	6 months	Herbicides (propazine and chlorthal dimethyl) affected mycorrhizal composition. Impact of herbicide varied with mycorrhizal species and concentration. High concentrations reduced mycorrhizal development and root growth. Low concentrations of chlorthal had positive impact.	Marks and Becker 1990

Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
				Mycorrhizas—succession				
Pinus radiata	Exotic	*Suillus* spp. *Tuber* spp.	New Zealand	0–4 yr	Nursery and forest	4 yr	Mycorrhizal composition sometimes changed after transplanting seedlings from nursery to forest. Related to soil type and fertility.	Chu-Chou and Grace 1988
Eucalyptus dumosa	Native	*Glomus* sp.	New South Wales, Australia	2–5 months	Pot experiment	5 months	Succession of VAM to EM in calcium carbonate soils. Improved growth and P uptake with inoculation	Lapeyrie and Chilvers 1985 and Chilvers et al. 1987
Eucalyptus marginata *E. diversicolor* *Acacia pulchella* *Banksia grandis*	Native	*Glomus fasciculatus*	Western Australia	4 months	Pot experiment	4 months	Succession of VAM to EM. VAM infection favoured over EM after fire.	Malajczuk et al. 1981
Eucalyptus viminalis	Exotic	*Pisolithus tinctorius* *Scleroderma* spp.	Santa Catarina, Brazil	2–15 months	Plantation	9 months	Succession of VAM to EM	Mendonca Bellei et al. 1992

[a]VAM = vesicular arbuscular mycorrhizas; [b]EM = ectomycorrhizas; [c]P = phosphorus; n/a = not available.

Roots and Mycorrhizas in Management

The following section will attempt to summarise how roots and symbionts are affected by different management activities. Data used to develop the discussion are in Tables 8.1–8.4. Of the many stresses impinging upon ecosystems, the following can have strong effects on ecosystem health and total productivity: 1) insect pests and fungal pathogens; 2) management activities (i.e., fertilisation, pruning/thinning, herbicides, pesticides etc.); 3) heavy metal toxicity; 4) air pollution; and 5) stochastic factors (i.e., climatic variations, droughts, hurricanes).

The information presented in this chapter highlights some of the limitations in our current knowledge: 1) most mycorrhizal studies have used seedlings grown in pots in nurseries or greenhouses conditions, and do not explain processes in the field or for mature trees; 2) those root studies conducted in the field are few in number and represent only a few tree species; 3) most studies focused on examining one factor in isolation (e.g., P uptake by plants, or one mycorrhizae inoculated on a seedling) thus precluding many interacting factors that could modify their expression in the field (i.e. soil aluminium levels which immobilise P in the field); 4) the short duration of the studies (especially with mycorrhizal fungi which typically were of several months duration) which is not relevant to long-term processes; and 5) studies concentrated on exotic species without understanding if and how they differed from native species, and on using 'superior' trees and mycorrhizal symbionts based on their ability to extract nutrients or protect seedlings from pathogens under laboratory conditions.

Fungal pathogens and insect pests

Many large-scale plantation projects (see Chapter 11) have been successful so far in obtaining high yields from fast-growing tree species but their long-term sustainability has not yet been assessed. The fact that plantation trials do not always result in the successful establishment of the desired plant species (due to either serious fungal disease or insect pest outbreaks and/or inherent abiotic site factors reducing or eliminating productivity) suggests the importance of having a better understanding of what controls the health and growth of these systems at a holistic level and in the long term (Trappe et al. 1984; Jorgensen and Wells 1986; Waring 1987). For example, one large plantation project in the tropics (the Jari project in Para, Brazil), started more than 20 yr ago, had to dramatically change the plant species and management strategies used due to pest and disease problems (Fearnside and Rankin 1985; Russel 1987; Fearnside 1988).

Tropical plantations may be highly susceptible to fungal pathogens and insect pests (Perry and Maghembe 1989; Wormald 1992). However, many of the data are observational and good documentation of cause-and-effect relationships is difficult to find for the tropics. The temperate zone studies suggest some possible explanations for the susceptibility of tropical plantations to diseases and pests, and also to help identify variables that might be sensitive indicators of stand health. For example, there may be a legacy of fungal diseases (coarse root fragments infected with root rot fungi, Chavez et al. 1980) that remain on a site which are capable of eliminating young trees planted after harvesting. The use of more genetically-uniform trees in a plantation may result in a greater proportion of the trees being susceptible to introduced insect pests or diseases. Seedlings may have been out planted with an introduced mycorrhizal fungus which was ineffective in protecting the plants against native disease organisms. Nitrogen fertilisation can cause shifts in carbon allocation away from plant secondary defensive chemicals and at the same time increase the palatability of leaves to herbivores. The structure of plantations often does not maintain the population of predatory insects that could help protect plants by containing pests (Schowalter and Means 1989).

Some studies have shown mycorrhizal fungi to be very effective at preventing the infection of plant roots by pathogenic fungi (Marx 1973). In laboratory experiments using agar plate tests, mycorrhizal fungi were shown to inhibit the growth of certain root pathogenic fungi and soil bacteria (Marx 1969). In pot experiments, mycorrhizal plants exhibited greater disease resistance and survival, once infected by pathogenic fungi, than non-mycorrhizal plants (Table 8.4). Thomas (1988) reported an inverse relationship between the degree of VA mycorrhizal colonisation of coconut palm roots *(Cocos nucifera)* and the population of VA spores in the soil, and the degree of root rot on palm roots. Maintaining healthy VA mycorrhizal populations in the soil may be critical in mixed planting situations. Plants maintaining healthy mycorrhizal populations should be used to identify which plant to intercrop in a plantation as a means of maintaining mycorrhizal inoculum potential over long-term plantation cycles (Waidyanatha 1980; Thomas 1988).

Research should also determine how much of the effect of mycorrhizal fungi is a nutrient effect and whether appropriate fertilisation can result in similar plant responses. Enhanced resistance of mycorrhizal plants to disease may be largely due to indirect effects of improving plant nutrition and health which would confer decreased susceptibility to attack by pathogens. Little is known about the effectiveness of different mycorrhizal species in protecting plants against many types of pathogens. However, since the contribution of a mycorrhizal species to plant performance probably varies with the physical and biotic environment (Perry et al. 1987), it is also likely that mycorrhizal species will have varying effects on plant responses to different pathogens.

Heavy metal toxicity

Heavy metals, particularly zinc, nickel, aluminium and copper, have detrimental effects on plant growth when present beyond critical levels (Kabata-Pendias and

Pendias 1984). Since some soils in the wet tropical zones have Al present at levels at which plant growth may be impaired (see Chapters 4 and 14), the mechanisms by which plants are able to avoid Al toxicity becomes relevant. Many native plants are well adapted to these metals and are accumulators of some of them (Goodland 1971) but exotic species may not have the same tolerance. This has been observed in the Amazon where the conversion of secondary forests to agricultural fields has required indigenous people to select agricultural crops tolerant of Al after initial crop failures (Pinedo-Vasquez, unpublished).

Some plants (tea, western and mountain hemlock) (Antonovics et al. 1971; Vogt et al. 1987a) are able to tolerate and accumulate heavy metals by sequestering them in non-biologically active tissues (Kabata-Pendias and Pendias 1984) while other plants are protected because the mycorrhizal associations on their roots either exclude metals or accumulate them within their mantle sheaths (Vogt et al. 1987a; Wilkins 1991). In the latter case, the plant shoots have significantly lower concentrations of the metals than non-tolerant species (Wilkins 1991). This is not unusual since fungi are known to be accumulators of many heavy metals and their reproductive structures (mushrooms) have been collected for chemical analyses to use as an indicator of pollution (Cromack et al. 1979; Vogt et al. 1992). There is evidence of a high degree of specificity between different mycorrhizal fungal species and their effect on plant tolerance against different metals (Jones and Hutchinson 1988). The high acidity of many tropical soils makes them often prone to Al and Mn toxicity and low P availability, so that mycorrhizas may be particularly important for plant growth in these environments.

Limited information is available on the effects of, and the response to, heavy metals in plantation ecosystems. Even in natural ecosystems (mainly in the temperate zone), the focus has been primarily on herbaceous species (Brown and Wilkins 1985), understanding the effect of increased Al cycling due to acid rain on vegetative communities or the links between vegetation and soil forming processes (Dahlgren et al. 1991). Preliminary studies suggest the importance of studying how Al toxicity varies by tree provenances since the tolerance of *Picea abies* to Al varied by provenances (Hodson and Wilkins 1989; Wilkins and Hodson 1989). No information is available on the effect of VA mycorrhizas on heavy metal tolerance (Wilkins 1991).

Management activities

In assessing the role of disturbance in natural and managed systems, it is important to consider the impact on both increasing and decreasing various types of environmental heterogeneity. If the imposed disturbance or management regime reduces belowground heterogeneity, this would have strong implications for the maintenance of healthy belowground ecosystems.

Fertilizers

Fertilizers are often an important input in plantation systems—not only is their application often required to increase and sustain production, but they are often applied at higher levels in order to enhance productivity (see Chapter 11). Excessive application of N or P fertilizers may alter mycorrhizal relationships between plant roots and microorganisms due to direct effects of high nutrient concentrations on microbial populations, or as a result of changes in the species composition or extent of colonisation of mycorrhizas caused by host regulation of the symbiosis in response to changed nutrient availability (see earlier section). Mycorrhizal colonisation on roots may decrease and their presence could ultimately be reduced or eliminated from the site as the capacity to maintain viable inoculum is reduced. Ikram et al. (1987, 1992) found that seedlings of *Calopogonium caeruleum* and *Hevea brasilensis* inoculated with VA mycorrhizas in the nursery exhibited less mycorrhizal root colonisation when soils were fertilised with P. The effect of P fertilisation on mycorrhizas is not simple and will vary with the original P content of the soil itself (Johnson 1993). For management purposes, it is important to know how the gradients of soil nutrients affect the degree of mycorrhizal colonisation of fine root systems and to identify threshold levels at which mycorrhizas are finally eliminated from root systems. The end result could be a plant that may have decreased growth due to metal toxicities or increased susceptibility to root pathogens (Marx 1969; Vogt et al. 1991a). How much of ecosystem resilience is directly linked to processes requiring strong root-microflora-soil interactions should be determined.

Pesticides and herbicides

Relatively few studies have been conducted on the potential effects of pesticides on roots or their associated microflora (Table 8.4). This could be important because pesticides can have unforeseen effects on non-target organisms which may influence productivity as much as or more so than the pests they are intended to control (Trappe et al. 1984). Effects of pesticides on mycorrhizal–plant interactions is one potential source of declining health and productivity of plantations which requires greater attention.

The few studies which have been conducted on pesticide–mycorrhizal interactions focus on isolated mycorrhizal species under highly controlled conditions and over short periods (Table 8.4). They indicate a high degree of variability in the effect of different pesticides and herbicides on different mycorrhizal species (Screenivasa and Bagyaraj 1989; Rouillon et al. 1989; Thapar and Uniyal 1990). Thapar and Uniyal (1990) studied the effect of four different pesticides (Aldrin, BHC, Furadon and Hexanema) on the growth of four species of ectomycorrhizal fungi, and reported that although all inhibited mycorrhizal formation in seedlings, they varied in their degree of toxicity and in the concentration required for toxic effects to occur. Screenivasa and Bagyaraj (1989) examined the effect of 9 fungicides, 3 nematicides and 5 insecticides at the recommended and at half the recommended levels on the growth of VA fungi in pot cultures and the effectiveness of the symbionts in reducing contaminant uptake. All were found to have a deleterious effect on VAM fungi at the recommended level. Interestingly, two of the chemicals, when given at half the recommended level, not only suppressed the contaminants but also improved VA mycorrhizal colonisation of roots, which Screenivasa and Bagyaraj (1989) attributed to reduced competition for space and nutrients between VA fungi and the contaminants. Similar mixed stimulatory/inhibitory effects have been reported in other studies (Iloba 1976).

Results of a few studies also indicate variable effects of herbicides on mycorrhizas. Sidhu and Chakravarty (1990) and Chakravarty and Chatarpaul (1988) indicated that with increasing seedling age, toxicity of herbicides was reduced. Increased degradation of herbicides in the field by soil microorganisms reduced the toxicity of herbicides compared to lab and greenhouse conditions. In-vitro studies by Rouillon et al. (1989) also indicate the ability of some mycorrhizas to degrade herbicides. The effect of herbicides on roots also directly affects mycorrhizal health. Herbicides have been reported to inhibit short root growth (more so than shoot growth) along with mycorrhizal formation and it is speculated that seedling production of glucose and belowground allocation is directly affected by herbicides. The complexity of interactions and herbicidal effects on the system is also indicated by Kassaby and Hepworth's study (1987) on the fungal root disease *Phytophthora cinnamomi* where the disease was found to be reduced or stimulated by different herbicides.

Thinning

Canopy architecture is known to affect dry matter partitioning among aboveground components (Linder and Rook 1984; Cannell 1985; Ford 1985), and provides an important justification for thinning practices in forest management. Very little is understood about the potential effects of thinning on carbon allocation between above and belowground sinks. Santantonio and Santantonio (1987) showed that thinning reduced fine-root longevity and increased the relative turnover rate by a factor of 2.4, and did not appear to provide a means for shifting production to another component, such as stem wood.

Soil disturbance

Most of the research on the effects of management-induced soil disturbance on the belowground system has focused on quantifying losses of organic matter and nutrients from erosion and leaching processes, and the risks associated with landslides under different management practices. There exists a good data base for this from temperate ecosystems (Edmonds et al. 1989). Most of the research in the tropics has concentrated on examining postharvest effects on the system (see Chapters 5 and 10). In general, roots are less likely to be affected than the forest floor during manual timber harvest operations, while mechanical site operations may seriously affect the root system and its nutrient storing and recycling capacity.

Studies in temperate regions have suggested that soil disturbance can reduce mycorrhizal populations by breaking up hyphal connections, eliminating inoculum and consequently affecting vegetation recovery (Perry et al. 1987). Loss of organic matter may also reduce mycorrhizal populations since hyphae are usually concentrated in areas of high organic matter, and lack of organic matter may reduce the availability of microsites suitable for sustaining mycorrhizas (St John et al. 1983; Vogt et al. 1995a). Studies in temperate regions have also specifically assessed the impact of soil compaction, nutrient leaching, organic matter loss, root strength and slope stability on root growth, generally showing a clear relationship between soil disturbance and decreased root growth (Ziemer and Swanston 1977; Ziemer 1981; Ruark et al. 1982; Petersson and Messing 1987). Roots have been found to positively affect soil physical conditions (decrease soil compaction, decrease soil erosion) when plantations were planted on abandoned pastures (Montagnini et al. 1991; McGroddy 1994). Similarly, VA mycorrhizas are usually reduced by various forms of soil disturbance, including strip mining (Allen and Allen 1980), soil erosion (Powell 1980) and mechanical disruption (Moorman and Reeves 1979; Reeves et al. 1979; Doerr et al. 1984; Cuenca and Lovera 1991). Species diversity of mycorrhizal populations may also be reduced and/or altered (Cuenca and Lovera 1991) and should be examined in greater detail.

Synthesis

A survey of research conducted on mycorrhizas in plantations suggests that much of the research was aimed at finding a 'super-symbiont' for inoculating plantation species (Table 8.4). The research sought to identify those symbionts which resulted in the greatest increases in seedling growth and to compare the ability of exotic and native fungal inoculants to increase plant growth (Lapeyrie and Chilvers 1985; Martinez-Amores et al. 1991; Ikram et al. 1992). Since many plantation tree species are exotic (Table 8.4), the focus on testing exotic symbiotic fungi is obvious—frequently areas being planted to exotic species do not have any of the appropriate mycorrhizal fungi present although seedling survival depends on these associations (Valdés 1986; Michelsen 1992). Most inoculation studies have concentrated on determining the effect of a single symbiont on seedling establishment and growth within the first 6–12 months following the outplanting (Table 8.4; Ikram et al. 1987).

Several studies have examined the replacement of nursery inoculum with indigenous mycorrhizal species following outplanting to the field (Lapeyrie and Chilvers

1985; Chilvers et al. 1987; Mendonca Bellei et al. 1992; Richter and Bruhn 1993) and the successional replacement of VA fungi by ectomycorrhizal fungi on roots (Table 8.4). How relevant these studies are for changes in fungal species in plantations over longer time scales is not known. More information is needed on interaction—both synergistic and antagonistic—between mixed-species communities of microorganisms, and on successional change within these communities in response to environmental change in plantations.

Inoculation of seedlings with ectomycorrhizas or VA mycorrhizas in the nursery has been shown to enhance initial seedling establishment and growth in the field, probably through the advantage conferred to seedlings by enhanced nutrition during this critical period (Janos 1980; Marx 1980). The positive effects of inoculation may also be explained by the often-low inoculum potential of nursery soils due to fumigation practices, collection of soil from areas depleted of mycorrhizas, or, in the case of exotic ectomycorrhizal species, the lack of colonising fungi in native soils (Marks and Kozlowski 1973). It is clear that inoculation trials with pure cultures of different fungal species can yield positive results in identifying fungi which have particular superior performance in the field (Valdés 1986; Ikram et al. 1987; Sieverding and Toro 1987; Burgess and Malajczuk 1989). Under natural conditions, however, trees are typically colonised by a wide array of different mycorrhizal species, and often by different types of mycorrhizas as well. This high diversity in the mycosphere may be crucial in buffering the system against disturbances or even fluctuations in the environment. However, only a few studies have assessed the performance of inoculation with mixtures of known species of mycorrhizas (Azizah and Martin 1992) or mycorrhizas in combination with other symbionts (Ramirez-Saad et al. 1992), and generally have not compared mixed with pure cultures, or different combinations of species. More common has been inoculation with field mixtures of indigenous mycorrhizas found in soil collected from suitable areas (Table 8.4; Sidhu and Behl 1992) and the identification of field mixtures with the greatest inoculum potential and most effect on plant growth (Asbjornsen and Montagnini 1994).

Most research on root–mycorrhizal–plant relations in tropical plantations has focused on seedlings in laboratory or shadehouse conditions with short time scales (6–12 months) and rarely includes follow-up studies or comparisons with mature trees. Although seedling establishment and growth are critical in terms of overall plant development, and stress due to transplanting shock may be high (Nambiar 1983), the belowground system continues to have an important function throughout the life of the plantation. Furthermore, since the life of a plantation may be 20–40 yr or longer, plants will be exposed to a dynamic and changing environment over extended periods.

More recent studies have begun to address other belowground aspects, for example, the processes of shifting carbon allocation, and improving techniques for isolating and testing effective mycorrhizal fungal species (Table 8.1–8.4). Research should address several issues: 1) multiple species interactions; 2) differences between seedling and adult tree responses; 3) exotic vs. indigenous species (both for trees and mycorrhizas and their ecosystem attributes); 4) diversity and ecosystem resilience and the role of roots and mycorrhizas in contributing to these; 5) carbon allocation and implications for ecosystem function, and how exotic and native species vary in the allocation of carbon to belowground components; 6) implications for agroforestry systems when plants are selected to maximise the use of nutrients in deeper soil horizons; 7) effects of nitrogen-fixing tree species on soil organic matter storage in addition to the nutrient effects; 8) identification of situations in which management practices are unable to compensate for abiotic or biotic changes in the environment and how belowground processes may compensate for these changes; and 9) how belowground elements contribute to ecosystem carbon and nutrient cycles.

Management practices are a key facet of the plantation environment through their effects on disturbance regimes, nutrient cycling, stand structure and diversity, and concentration of metals and chemicals in the soil, to name a few. Although intensive human activities may unavoidably increase the level of stress in the ecosystem, management can also help to enhance ecosystem resilience and resistance to stress through judicious manipulation. These approaches need to be expanded to include techniques which create conditions to favour a healthy belowground system in the long term. For example, techniques that enhance belowground heterogeneity, thus creating a more diverse mycorrhizal community, and which use fertilizers and pesticides wisely based on sound knowledge about the indirect effects on symbiotic associations, can contribute to the long-term productivity of the ecosystem.

In order to achieve this, we need to learn how natural systems maintain their resistance and resilience to disturbances. Many of the disturbances that a plant will be exposed to will be detected and responded to by roots and mycorrhizas before any symptoms become apparent aboveground (Vogt et al. 1993). Mycorrhizas may buffer the ecosystem against environmental stress and greatly enhance resiliency by, for example, increasing uptake of nutrients when available and releasing them from storage when they are scarce, or by preventing infection by root pathogens during times when the plant is susceptible to stresses (Marks and Kozlowski 1973; Vogt et al. 1991a). It is important to increase our understanding of when and how roots and mycorrhizas function in ecosystems to sustain plant growth over longer time scales. This type of information can then be used to determine the trade-offs between management options.

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9

Nitrogen Fixation in Tropical Forest Plantations

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Abstract

Nitrogen (N) fixation by trees involves the symbiotic relationship between certain tree species, N-fixing microsymbionts and mycorrhizal fungi. Under tropical conditions, many N-fixing trees exhibit rapid growth and biomass accumulation, and enrich soil in total and available N. Most species currently in use come from four genera: *Casuarina*, *Albizia* (including *Paraserianthes*), *Leucaena* and *Acacia*. Nitrogen fixation typically supplies 40% to 80% of the N used by these trees, with input rates of 50 to 150 kg N $\text{ha}^{-1}\ \text{yr}^{-1}$ for vigorous, well-stocked stands. Rates of N fixation probably depend on factors that affect overall tree performance, including water regime, soil nutrient supplies and the genetics of the trees and microsymbionts. Stands that contain N-fixing trees typically show higher rates of nutrient cycling (for all elements) than non-N-fixing stands. Little is known about the long-term changes in soil properties under the influence of N-fixing trees. As with other tree species, some cases have documented changes following stand establishment such as declines in soil pH and decreases in pools of labile P and exchangeable soil cations (despite higher annual rates of uptake and cycling). Much more work is needed to assess the long-term implications of changes in soil chemistry on fertility. The selection and use of N-fixing trees will depend on: 1) continued development of appropriate silvicultural methods (including fertilisation); 2) market-driven demands for wood and wood products from these species; and 3) the balance between soil improvement from increased N and any depletion of other nutrients under intensive management.

NITROGEN-FIXING TREES in tropical environments appear to offer both high rates of growth and soil enrichment. This view is often based on observations in the first rotation of a plantation, or on natural regeneration following disturbance. A wide variety of N-fixing trees is available for use in plantations, but only a handful have received much study for silviculture and management. Fewer still have been examined for rates of N fixation or effects on site fertility and nutrient cycling. In this review, we present brief descriptions of the major genera and species of N-fixing trees used in tropical plantations, discuss the factors that influence the rate of N fixation, and examine the subsequent effects of these trees on nutrient cycling. We then summarise patterns of growth for comparisons of N-fixing and non-N-fixing plantations, in monocultures and mixtures. Two case studies illustrate some key features of interactions between N fixation, tree production and nutrient cycling in monocultures and mixed stands. The chapter concludes by synthesising major silvicultural and research issues for harnessing N-fixation in tropical plantations.

Tropical N-fixing trees that are already used in plantations span several families, many genera and dozens of species, with a potential area of tens to hundreds of millions of hectares. Despite the current and potential magnitude of such plantations, information on the ecological and silvicultural aspects of these systems remains largely anecdotal (see MacDicken 1994 for a good summary, and Werner and Müller 1990 for many abstracts from around the tropics). Much more is known about the relatively few and less-widespread N-fixing trees in temperate forests. For example, all of the topics covered in this chapter were expanded into a full synthesis volume for a single temperate species (red alder, *Alnus rubra;* Hibbs et al. 1994) whose range covers just 1.4 million ha. We hope this chapter can outline the important issues in the use of N-fixing trees in tropical plantations, and provide a context for the extensive local work necessary to develop the potential of N-fixing trees in each region.

The Nitrogen Fixation Process

For at least 3.5 billion yr, certain prokaryotic microbes have been able to break the stable triple bond of atmospheric nitrogen (N_2), using the nitrogenase enzyme, to make biologically useable forms of nitrogen (Walker et al. 1983; Sprent 1987; Purves et al. 1992):

$$8H^+ + N_2 + 8e^- \rightarrow 2NH_3 + H_2$$

In all this time, no eukaryotic organisms have developed the ability to fix atmospheric nitrogen. Many plant species (and at least a few animal species, such as termites) have instead developed symbiotic, mutualistic relationships with prokaryotes. The most important symbioses for plantation forestry are between some tree species in the legume family (Faria et al. 1989; MacDicken 1994) and bacteria in the genera *Rhizobia* and *Bradyrhizobia*, and those between several other tree genera (such as *Casuarina*) and the filamentous bacteria (actinomycete) genus *Frankia* (Benson and Silvester 1993; MacDicken 1994). In both types of symbioses, specialised nodules develop on the tree roots to provide favourable environments for the N-fixing bacteria. The bacteria enjoy a supply of carbohydrates and microaerobic environments, and the roots receive a supply of reduced nitrogen for use in amino acids, proteins and other biochemicals. Once the fixed nitrogen is in organic compounds, it cycles through the ecosystem through litterfall, root death and decomposition. Some direct 'leaking' of fixed N from roots into the soil has been suggested, but no evidence of substantial losses from healthy roots is known.

Seedlings of N-fixing trees may be inoculated with the appropriate bacteria or actinomycete in the nursery, or simply infected by microbes that are widely present in soils. Many techniques are available, including: pure cultures of the microsymbiont, suspensions of macerated nodules, or simply suspensions of soil from existing plantations. Methods manuals are available, tailored for various species and regions (cf. Bergerson 1980; Silvester 1983; Sprent and Sprent 1990; Weaver and Danso 1994; Baker et al. 1996).

The Species

Over 600 species of trees have been reported to fix nitrogen (MacDicken 1994). Precise information on the current use of N-fixing trees in tropical plantations is not available. In 1980, N-fixing trees were planted on about 5% of all tropical plantation sites (Evans 1992), and their use has continued to increase. In 1990, *Acacia* species were planted on about 7% of all tropical sites (Chapter 1). Many N-fixing trees are well suited for plantation management in single-species, even-aged stands or in multispecies, multiage stands. However, most of the information available on growth, symbioses and nutrient cycling focuses on just four genera: *Casuarina*, *Albizia* (including *Paraserianthes*), *Leucaena* and *Acacia*. See MacDicken (1994) for a summary of available information on other genera and species. In this review, we do not include other important N-fixing species (such as *Gliricidia* spp.) that are used primarily in agroforestry (which is beyond our scope), nor dryland, multipurpose trees such as arid-land *Acacia* spp. and *Prosopis* spp.

Casuarina species belong to the Casuarinaceae, a dicotyledon family closely related to Betulaceae and Myricaceae. These species host N-fixing *Frankia* actinomycetes (filamentous bacteria), vesicular-arbuscular mycorrhizae (VAM), and also ectomycorrhizae (Reddell et al. 1986). Most of the 80 species in the genus originate from Australia, and the most widely planted species is *Casuarina equisetifolia*. Other commonly-used species include *Casuarina cunninghamiana*, *Casuarina glauca* and *Casuarina junghuniana* (National Research Council 1984a; Diem and Dommergues 1990; Parrotta 1993; MacDicken 1994; M. Paschke, pers. comm.). *Casuarina* wood is very dense, making excellent fuelwood and construction poles, but poor timber (because of warping and splitting on drying) and pulp (from difficulty in grinding). *Casuarina* trees are often used for land reclamation, sand dune stabilisation and wind breaks. Rates of nitrogen fixation have been reported of 60 to 95 kg N ha^{-1} yr^{-1} in pure stands, and 40 to 60 kg N ha^{-1} yr^{-1} in stands mixed with *Eucalyptus* (Table 9.1). Based on ^{15}N tracer techniques, *Casuarina* seedlings and stands typically obtain about two-thirds of their N from the atmosphere (Table 9.1). On good sites, annual wood increments are commonly between 15 and 20 m^3 ha^{-1} (10 to 15 t (dry) ha^{-1}; National Research Council 1979). *Casuarina* trees are tolerant of droughty soils and saline conditions, with widespread plantations in

Table 9.1 Nitrogen fixation estimates for tropical plantations

Species, location	Method	N fixation (kg ha^{-1} yr^{-1})	N fixation (% N derived from atmosphere)	Reference
Casuarina equisetifolia, Puerto Rico	In field ^{15}N soil enrichment, between 6 and 24 months	80–95 pure *Casuarina*, 40–60 in mixed *Cas./Euc.*	50–70	Parrotta et al. 1994a
C. equisetifolia, India	In field acetylene reduction, age 5 and 8 yr	90 (5 yr plantation) 60 (8 yr plantation)		Srivastava and Ambasht 1994
C. equisetifolia		60		Dommergues 1963
C. equisetifolia, Senegal	^{15}N natural abundance in 3-yr-old plantation	35–40	15	Mariotti et al. 1992
C. equisetifolia, Senegal	Accretion in forest floor and mineral soil over 34 yr	75		Mailly and Margolis 1992
Albizia falcataria, Hawaii	0-0.15 m soil N accretion in 12 yr	65–140		Garcia and Binkley, unpublished
Leucaena leucocephala, Puerto Rico	In field ^{15}N soil enrichment, between 6 and 24 months	50 to 70 in mixed plantations; 100 in monocultures	70–80	Parrotta et al. 1994b
L. leucocephala, Tanzania	Acetylene reduction in 4-yr-old plantation	110 ±30		Högberg and Kvarnström 1982
L. leucocephala, Nigeria	In field ^{15}N soil enrichment, 1 yr	150–180	40–45	Sanginga et al. 1989, 1994
L. leucocephala, 7-month-old mixed plantations with *Eucalyptus*	Soil ^{15}N enrichment	45 kg ha^{-1}/7 months	26–67	Baker et al. 1992
Albizia falcataria, 7-month-old mixed plantations with *Eucalyptus*	Soil ^{15}N enrichment	70 kg ha^{-1}/7 months		Baker et al. 1992
Albizia lebbek, Puerto Rico	Accretion in vegetation and 0–20 cm soil, 4.5 yr	260		Parrotta 1992c
Alnus nepalensis, India	Acetylene reduction, 7- to 56-yr-old stands	30 – 120		Sharma and Ambasht 1988
Alnus jorullensis, Columbia	2-yr plantation, extrapolated soil accretion estimate	280		Carlson and Dawson 1985
Stryphnodendron microstachyum, Costa Rica	Soil ^{15}N enrichment, 18 months and 22 months		50–60	Baker and Montagnini 1994

areas such as Egypt (El-Lakany, Turnbull and Brewbaker 1990). An impressive planting program in southern China has developed a shelterbelt stretching 3000 km (0.5 to 5 km in width; National Research Council 1984a). Casuarinas can grow under a broad range of conditions, from <500 mm of rain yr^{-1} to more than 5000 mm yr^{-1}, and from mildly acid to alkaline and saline soils. These species are easy to propagate; the risk of *Casuarina* becoming a weedy invader is high.

Most N-fixing species belong to the Fabaceae (legume family), which is comprised of three subfamilies. About 90% to 95% of the species in the Mimosoideae and Papilionoideae fix nitrogen, compared with about 25% of the species in the Caesalpinioideae (Brewbaker 1990).

Albizia species belong to the Mimosoideae subfamily. The most commonly used species is *A. falcataria* (native to the eastern islands of the Indonesian archipelago), which is now classified as *Paraserianthes falcataria* (this species will be included with *Albizia* in this paper). Albizias are nodulated by *Rhizobia* and *Bradyrhizobia* bacteria (Turk and Keyser 1992) and host VA mycorrhizae. About 100 species comprise the genera of *Albizia* and *Paraserianthes*, but only three (*A. falcataria*, *A. lebbek* and *A. procera*) have been widely used in tropical plantations (National Research Council 1979; MacDicken 1994). Surprisingly few estimates of N fixation are available for *Albizia*, but rates are probably comparable to other leguminous trees (Table 9.1). The wood of *Albizia* is used for fuel, pulp, light construction, furniture, panelling, cabinets, toys, musical instruments, particle board and pallets (Parrotta 1987a, b, 1990; Seorianegara and Lemmens 1993). Imports of *Albizia* wood to Japan are particularly high (Seorianegara and Lemmens 1993). *Albizia* foliage is often used for livestock fodder. The annual increment in plantations ranges from about 20 to 50 m^3 ha^{-1} (6 to 13 t ha^{-1} dry weight) for average sites, and up to 55 m^3 ha^{-1} (18 t ha^{-1}) for the best sites (National Research Council 1984a; Domingo 1983; Binkley et al. 1992; Seorianegara and Lemmens 1993). Albizias grow well with at least 1200-1500 mm yr^{-1} of rain and tolerate acid soils well (to at least pH 4.5). Wind damage may be severe in some cases. Albizias are easy to propagate and may invade local communities near plantations; *A. procera* has invaded many abandoned agricultural fields and roadsides in Puerto Rico (Parrotta 1987a).

Leucaena leucocephala (the only one of 16 species in the genus to be widely used) may be the most famous N-fixing tree in the tropics, often hailed as a miracle tree (National Research Council 1984b; Parrotta 1992a; MacDicken 1994). The genus (from the Mimosoideae subfamily of the Fabaceae) is originally native to Central America, but was spread by Spanish expeditions to the Philippines and other areas more than 200 yr ago. Other *Leucaena* species may warrant intensive development for plantation use, including hybrid lines (Gathaara et al. 1991; Brewbaker and Sorensson 1994). *Rhizobia* bacteria nodulate *Leucaena*, and VA mycorrhizae also infect *Leucaena* roots. About half of the N required by *Leucaena* comes from N fixation (Table 9.1), with typical rates of 100 to 150 kg N ha^{-1} yr^{-1}. The wood is used for fuel, roundwood (poles and posts), saw timber and pulp. *Leucaena* tolerates drought well and dominates some communities on Oahu, Hawaii, where precipitation averages only 250 mm yr^{-1} (National Research Council 1984b). However, 1000 to 3000 mm yr^{-1} of rain are required for suitable plantation growth. Annual stemwood increments range from about 10 to 60 m^3 ha^{-1} (5 to 30 t ha^{-1}; Domingo 1983). *Leucaena* is intolerant of acid soils, and grows best in soils with pH >6.0. Some species, such as *Leucaena diversifolia*, are very tolerant of cold and perform well in subtropical environments such as Argentina (F. Montagnini, pers. comm.).

The genus *Acacia* (also subfamily Mimosoideae of the Fabaceae) is one of the largest genera in the legume family, containing about 1200 species. Acacia trees house nitrogen-fixing *Bradyrhizobia* (Galiana et al. 1990) or *Rhizobia* (Turk and Keyser 1992), and are infected by VA mycorrhizae. We are aware of no estimates of N-fixation from the commonly used plantation trees: *A. melanoxylon* (Australian blackwood), *A. mollissima* (black wattle), *A. auriculiformis*, *A. mearnsii* and especially *A. mangium* (mangium). Mangium originates from coastal Queensland in Australia, Papua New Guinea and eastern Indonesia. The wood is used for furniture, finishing timber, veneer and light-duty building material, and may be suitable for both fuelwood and pulp (National Research Council 1983; MacDicken 1994). Annual increments in plantations typically range from 20 to 40 m^3 ha^{-1} (11 to 22 t ha^{-1}), up to 50 m^3 ha^{-1} (28 t ha^{-1}) on the best sites. Mangium requires high rainfall (typically >2000 mm yr^{-1}), and mildly to strongly acidic soils (down to pH 4.5).

In some cases, herbaceous or shrubby N-fixers may be used in the early stages of plantation development to provide N to crop trees. A famous example is the establishment of radiata pine (*Pinus radiata*) on sand dunes in northern New Zealand, with N supplied by lupins (*Lupinus arboreus*). Tree basal area was substantially higher in plots with lupins; additional inputs of fertilizer N further increased tree growth (Gadgil 1983). A variety of studies have examined the use of herbaceous legumes in pine plantations in New Zealand and Australia. In some cases, tree growth is enhanced by the N-fixer, as a result of either improved nutrition or decreased competition from other noncrop vegetation. As with N-fixing trees, the benefits to intercropped non-N-fixing trees depend on enhancement of tree nutrition (most valuable on N-limited sites), and competition for other resources (particularly water). In many tropical cases, the time to canopy closure is very short (from 1 to 3 yr), so underplanted N-fixers may have only a brief window for vigorous growth and N fixation compared to temperate situations where canopy closure typically takes 5 to 20 yr or more. This short window of opportunity for including non-tree N-fixers in mixed plantations might be expanded by alternating crops, with the N-fixer (perhaps an agricultural legume) grown for several years between rotations of crop trees. To our knowledge, this alternate rotation system has not been tested in the tropics, and experimentation is warranted.

Rates of N Fixation

Table 9.1 tabulates rates of N fixation from a wide range of studies, species and experimental situations. The data are presented in two forms. From a soil and ecosystem perspective, the quantity of N fixed per hectare (kg N ha^{-1} yr^{-1}) may be most interesting. From the perspective of the nutrition of the N-fixing trees, the percentage of the N supply of a tree that is derived from the atmosphere (%Ndfa) may be more interesting. Rates of N-fixation are highly variable, and depend on the main effects and interactions of the genetics of the host, the microsymbionts and environmental conditions.

Four approaches are used for estimating rates of N fixation in plantations: N accretion, acetylene reduction, ^{15}N natural abundance and ^{15}N labelling (Silvester 1983; Reporter 1985; Caldwell and Virginia 1991). Nitrogen accretion is determined by examining changes in the total N content of a stand, or contrasting the total N content of an N-fixing stand with a non-N-fixing stand. For example, soils under 12-yr-old *Albizia falcataria* plantations in Hawaii had 1.0% N in the top 15 cm of soil, compared with 0.8% N for soils under *Eucalyptus saligna* (Garcia and Binkley, unpublished). The greater N in *Albizia* soils extrapolates to an increase of about 1000 kg N ha^{-1}, or about 80 kg N ha^{-1} yr^{-1} of accretion in this soil layer. Inclusion of the extra N in biomass and deeper soil horizons would increase the annual rate of accretion to more than 100 kg N ha^{-1} yr^{-1}. Estimates of accretion may under-represent the actual rate of fixation if losses of N (through leaching of nitrate, or denitrification) are substantial. These estimates also gauge the total input of N across the life of the stand and may not represent current activity.

The acetylene reduction approach takes advantage of the nitrogenase enzyme's preference for reducing acetylene to ethylene ($C_2H_2 + 2H \rightarrow C_2H_4$) over reducing dinitrogen to ammonia. In this approach, nodules are excavated from the soil, incubated in a closed jar (or flow-through gas system) with acetylene and then the ethylene produced is measured by gas chromatography. A conversion from acetylene reduced to N_2 reduced may be applied. Rates may be scaled up to the stand level by estimating the nodule activity rate throughout the diurnal and annual cycles and by multiplying by the nodule mass per area. This approach is subject to many uncertainties, including the effect of acetylene on nitrogenase activity and the uncertainties in variation in rates and nodule mass (Silvester 1983; Chalk 1985; Winship and Tjepkema 1990). Acetylene reduction may or may not provide quantitative estimates of N-fixation, but this approach is well suited for examining patterns of variation. For example, Srivastava and Ambasht (1994) used acetylene reduction to document seasonal patterns in N-fixation rates in 5- and 8-yr-old plantations of *Casuarina equisetifolia*, focusing on changes induced by soil moisture regimes.

Nitrogen from fixation has a ratio of stable isotopes (^{15}N:^{14}N) that is similar to the ratio in the atmosphere, whereas the natural abundance of these isotopes in soils often shows enrichment of ^{15}N. Where the isotope ratio of newly-fixed N differs from the 'prior' N, these ratio differences can be used to estimate the rate of N fixation, as well as the addition of newly-fixed N to various ecosystem pools. The small differences in isotope ratios are usually reported as σ^{15}N, which is the parts-per-thousand enrichment in ^{15}N of the sample relative to the ratio in the atmosphere. The use of this method requires:

1) a sufficient enrichment or depletion of the 'prior' ecosystem N relative to atmospheric N (a difference of $\pm$ 5 σ^{15}N is usually the minimum needed);
2) an accurate measure of the σ^{15}N of the plant-available portion of the 'prior' N (typically obtained from a non-N-fixing species growing on the same or similar soil); and
3) no substantial (or biasing) discrimination between the N isotopes in other ecosystem fluxes (such as denitrification).

These assumptions warrant careful evaluation in each study. As an example of the σ^{15}N approach, Hamilton et al. (1993) examined the isotope ratios in stands where understorey *Acacia melanoxylon* and *Acacia mucronata* were established after a light ground fire in a *Eucalyptus* forest. The σ^{15}N in non-N-fixing grass was used to represent the 'prior' N, with a value of +15.8 ‰ excess of ^{15}N (the concentration of ^{15}N was 15.8 parts per thousand higher than in the atmosphere). The ^{15}N values for the acacias fell between 8 and 9 σ^{15}N, indicating that about half of the acacia's N supply came from the atmosphere (with 0 σ^{15}N) and half from the 'old' N in the soil (with σ^{15}N of about 16). Multiplication of this percent of N derived from the atmosphere (%Ndfa) times the N content of the acacias gave an N fixation rate of about 5 g ha^{-1} yr^{-1} (*A. mucronata*) to 116 g ha^{-1} yr^{-1} (*A. melanoxylon*). These rates were very low because of small plant size and low plant density.

The 'prior' soil pool of N may also be labelled through addition of ^{15}N and any additional N provided by N fixation then dilutes the ratio of ^{15}N:^{14}N. This approach is expensive, but not beyond the reach of many research budgets (Baker et al. 1996). A key to accurate estimates of N fixation is obtaining a precise and accurate estimate of the ^{15}N concentration in non-N-fixing plants. In some cases, soils may be 'double labelled' with ^{15}N and ^{35}S (cf. Hamilton et al. 1993); if the N-fixing and non-N-fixing species show the same sampling of the soil S isotopes, then they may be sampling comparable portions of the soil's available N pools.

Factors Influencing Rates of N Fixation

The process of symbiotic N fixation generally depends on the overall vigour and productivity of the host plant. Environmental conditions that favour tree growth should favour higher rates of N fixation, including adequate water and temperature, high supplies of soil nutrients such as P and Ca and favourable soil pH. As noted below, any role of the supply of readily available N in the soil on rates of N fixation remains unclear. Mycorrhizal symbioses also appear to be very important and genetic variation in all members of the symbioses (host, N-fixing bacteria and mycorrhizal fungi) may affect rates of N fixation. At a hectare scale, the number of N-fixing trees may or may not influence the amount of N fixation per hectare. At low densities of N-fixing trees per hectare, N fixation is probably low; the trend in N fixation (kg ha^{-1} yr^{-1}) across a range of tree stocking densities remains largely unknown.

Soil factors

Nitrogen fixation activity of trees appears to be tightly coupled with adequate plant moisture conditions. Low supplies of water may affect N fixation by lowering plant carbohydrate supply, carbohydrate transportation to the nodules, or direct impairment of nodule development and activity (Dixon and Wheeler 1983). For example, Srivastava and Abasht (1994) found that *Casuarina* nodule mass increased by fourfold from the end of the dry season (June) into the wet season (July and August) in Egypt. Specific nodule activity (as gauged by acetylene reduction per gram of nodule) also increased severalfold with the increase in soil moisture, so that the N-fixation rate increased by almost 10-fold with the coming of the rains. Soil moisture variations accounted for about 80% of the variation in N-fixation rates.

Soil aeration

Some *Casuarina* species may be notably tolerant of waterlogging, owing to aerenchyma in roots. For example, van der Moezel et al. (1988) found that 3 months of waterlogging of *C. obesa* seedlings reduced plant growth by only 15% relative to well-aerated controls. Interestingly, these seedlings also tolerated high solution salinity (up to 10% of seawater salinity) with only a 40% reduction in growth.

Soil P supply

Nitrogen-fixing plants generally have a high demand for phosphorus (Marschner 1986; Israel 1987) and this appears to hold for tropical N-fixing trees. It is not clear if this high demand for P relates directly to the N-fixation process, or simply to overall plant nutrition. We know of no studies that manipulated P supplies in plantations of N-fixing trees to test for any response of N fixation. One study correlated the biomass of individual, 7-month-old *Leucaena leucocephala* trees in a field plantation with soil properties under each tree (Crespo and Curbelo 1991). This study found that tree size correlated weakly with soil pH ($r^2 = 0.3$) and available P ($r^2=0.1$).

Many glasshouse studies, however, have documented significant responses of N fixation to P fertilisation for tropical tree seedlings. Sanginga et al. (1991) examined growth of *Leucaena leucocephala* in a pot study with 2 levels of P fertilisation (20 and 80 mg P kg^{-1} soil). Total seedling weight at the higher P level was about 8% more than at the lower level, with a greater increase in root mass than in shoot mass. In a second study with 5 levels of P fertilisation (from 0 to 80 mg P kg^{-1} of dry soil), nodule biomass increased with increasing P addition, from 26 mg $plant^{-1}$ in the 0 P treatment to 400 in the 80 mg P kg^{-1} soil treatment. However, N fixation rates differed much less, ranging only from 40 mg N $plant^{-1}$ for 0 P, to 53 mg N $plant^{-1}$ for P rates of 40, 60 and 80 mg kg^{-1}. The percent of the seedling N obtained from the atmosphere was constant across P fertilisation regimes, ranging in a narrow span of 59% to 64%. Sanginga et al. (1991) concluded that the major effects of P on N fixation derived from the overall benefit of P to plant growth (particularly to root growth and root infection) rather than from a direct effect of P supply on the N-fixation process per se.

In contrast to these results for *L. leucocephala*, Sun et al. (1992) found that although *Acacia mangium* growth was maximised with about 10 mg P kg^{-1} of dry quartz sand in pots, N fixation continued to increase with rates of P application up to at least 30 mg P kg^{-1} sand.

The supply of P to trees may depend heavily on soil pH and exchangeable aluminium. Again, insights are available only from glasshouse studies. Duguma et al. (1988) examined the growth of *Leucaena leucocephala* in response to fertilisation with P versus liming. They found that plant growth (and P nutrition) could be substantially improved by either soil treatment. Naidu et al. (1990) also examined the response of *Leucaena* to additions of P or lime in four acidic soils from Fiji. The P extractable by anion exchange resins (a good index of plant-available P) increased in response to liming up to pH 5.2 and then declined, indicating a maximum P supply at about pH 5.2. This corresponded to the pH where maximum growth was achieved and where exchangeable aluminium reached 0. Additions of P also increased seedling growth. Umali-Garcia et al. (1988) found that the optimum pH for *A. mangium* was higher than 5.8; soils limed to pH 6.5 produced twice the seedling growth of pH 5.8 control soils.

Soil N supply

It would seem that N-fixing plants should expend energy on N fixation only when the supplies of soil N are low; with high soil supplies of ammonium and nitrate, N fixation should be reduced or eliminated (e.g. Marschner 1986; MacDicken 1994). The data are fairly convincing for agricultural legumes in highly fertile soils, but the evidence is scanty for N-fixing tropical trees (Sprent 1994). As an example, Ingestad (1980) found that increasing supplies of nitrate *increased* N-fixation by grey alder (*Alnus incana* (L.)) when the supply was provided at low concentrations and applied frequently. Binkley et al. (1994) reviewed studies of N fixation by temperate red alder (*Alnus rubra* Bong.) and found no evidence of suppression of N fixation by levels of ammonium or nitrate commonly found in soils. In situations with low soil N supplies, N-fixing seedlings often benefit from N fertilisation (cf. Cobbina 1991) and some evidence indicates that N fixation may be enhanced with additions of ammonium or nitrate (e.g. Reinsvold and Pope 1987; Binkley et al. 1994; Sprent 1994).

What data are available for tropical trees on the feedback of soil N and N fixation? Umali-Garcia et al. (1988) found that fertilisation of potted *Albizia falcataria* with the equivalent of 30 to 100 kg N ha^{-1} reduced nodule biomass by 10% to 60%, although nodule activity (and hence N fixation) was not examined. Sanginga et al. (1989) examined the effects of 40 and 80 kg N ha^{-1} of fertilizer on the mass of nodules on inoculated *Leucaena leucocephala* seedlings. Nitrogen fertilisation further reduced the nodule mass by about half and reduced N fixation by about the same amount as the N applied in the fertilizer. Goi et al. (1993) found that both nodulation and growth of *Acacia auriculiformis* were stimulated by ammonium additions, but impaired by nitrate additions. Arnone et al. (1994) performed a more precise pot experiment, where the root systems of individual *Casuarina cunninghamiana* were divided into separate halves of pots which were then irrigated with a low nitrate solution (0.05 mmol L^{-1}, = 0.7 mg N L^{-1}), or a high nitrate solution (3 mmol L^{-1}, = 42 mg N L^{-1}). The 'high' nitrate treatment used a concentration that was several times greater than that found in real soils, representing an extreme treatment. Roots experiencing the low nitrate treatment had substantial formation of root hairs and nodules, regardless of whether the other half of the root system was in a low or high nitrate treatment. Arnone et al. (1994) conclude that nitrate inhibits nodule initiation and development locally and that specific nitrogenase activity may be inhibited throughout a plant with a high N supply. van Kessel et al. (1994, see Fig. 9.1) found that the $^{15}N:^{14}N$ ratio in *Leucaena leucocephala* leaves declined with plantation age and Dommergues (1995) inferred that this pattern indicated a decline in N fixation as soil N supply increased. The same pattern would also result from increased N uptake from the soil after yr 2 as the trees fully occupied the soil (which would dilute the $^{15}N:^{14}N$ ratio even if N fixation remained high).

Taken together, these studies indicate that N fixation by tropical trees could decline as the supply of soil ammonium or nitrate increases. Some scientists are relatively convinced that N-fixation in tropical trees declines as soil N supplies increase (cf. Dommergues 1995), whereas others expect soil N supplies will rarely be high enough to reduce N fixation (P. Högberg, F. Montagnini, pers. comm.). We suggest that more evidence is needed before forming a general conclusion.

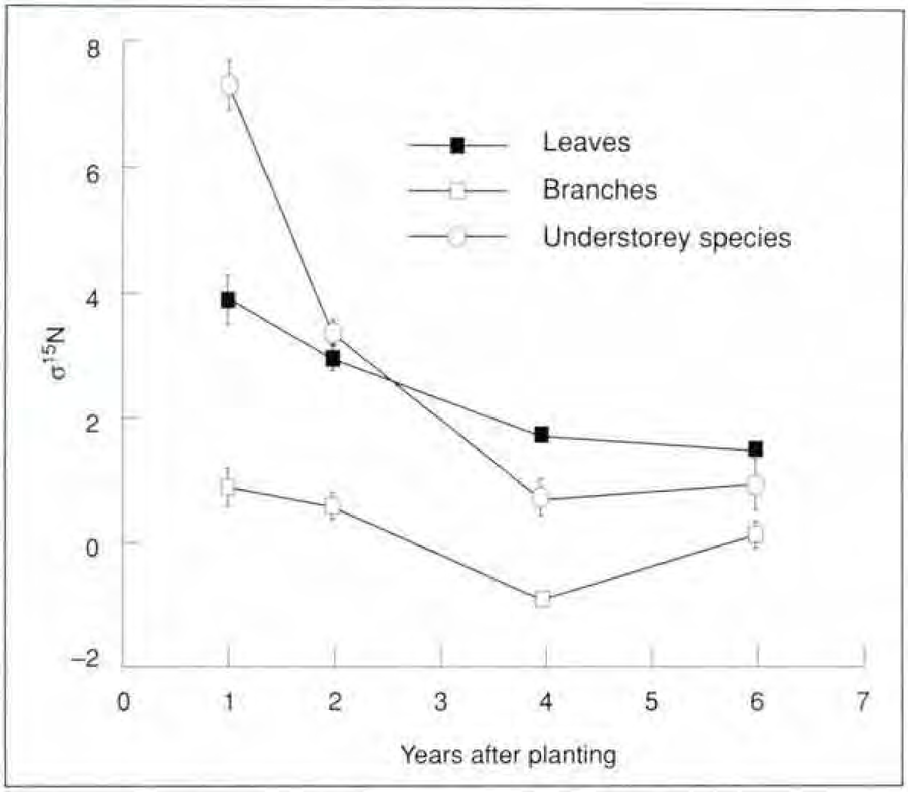

Figure 9.1 Changes in the natural abundance of ^{15}N (in ‰ difference from atmospheric ratio) for leaves and branches of *Leucaena leucocephala* and for associated understory species (from van Kessel et al. 1994)

Mycorrhizal associations

Tropical nitrogen-fixing trees clearly require mycorrhizal associations for normal growth and nitrogen fixation. The benefits may include improved growth, higher P uptake and perhaps increased drought resistance (for a tropical review, see Mason and Wilson 1994). Many studies have characterised the responses of growth, nodulation and N-fixation rates to mycorrhizal inoculation, typically with several species of mycorrhizae and varying soil nutrient treatments.

We can make few generalisations about the importance of inoculating seedlings before planting, about which fungi work best with which trees and how to optimise the tripartite symbiosis of tree, N-fixing bacteria and mycorrhizae. A typical example of the importance of mycorrhizae was shown in a glasshouse study in an artificial medium with *Casuarina equisetifolia* inoculated with 11 species of mycorrhizae (Vasanthakrishna and Bagyaraj 1993). Inoculated seedlings were 10% to 215% larger than uninoculated seedlings and the P content of inoculated seedlings was increased even more. A more extensive study with *Leucaena leucocephala* used real soil with a range of additions of P (Purcino et al. 1986). Inoculation with

Glomus species doubled seedling weight, increased both nodule weight and specific activity by 50% (resulting in more than double the N-fixation rate). Inoculated seedlings also took up twice as much P from the highly weathered soil and uptake of P in response to P fertilisation was greater for inoculated seedlings. Manjunath et al. (1989) also found that use of fertilizer P depended heavily on colonisation of *Leucaena leucocephala* by VA mycorrhizae. Habte and Musoko (1994) found that mycorrhizal inoculation improved growth of both *Albizia ferruginea* and *Enterolobium cyclocarpum* when the supply of P in the rooting medium was 0.012 to 0.02 mg P L^{-1} (a reasonable range for forest soils), but that mycorrhizal inoculation reduced the growth of both species at 0.2 mg P L^{-1} (a level never reached in forest soils?).

Much more work is needed to determine the benefits of inoculation of seedlings before outplanting (Torrey 1992; MacDicken 1994; Mason and Wilson 1994) and the insights gained from this work may be very specific for locations and species. Operationally, most tree species that are infected by VA mycorrhizae have no trouble finding inoculum in normal tropical soils (e.g. Sankaran et al. 1993).

Genetics of trees and symbionts

As with all plantations, the performance of tropical trees depends strongly on the provenance, family or genotype of the seedlings. For N-fixing trees, the genetic implications are more complicated owing to genetic variation in the N-fixing efficiency of the bacteria (Sprent 1994) and in some cases the highly significant interaction between the genotypes of the host tree and the bacteria. Adding in the effects (and interactions) of mycorrhizal species and strains results in innumerable possibilities. Examples below illustrate the importance of these features and the wide-ranging patterns of interactions.

The growth of 25 provenances of *Acacia auriculiformis* on seven sites in four countries showed strong interactions between provenance and sites (Awang et al. 1994). No intentional inoculation of *Rhizobia* or VAM was attempted, so it is impossible to separate the provenance and site effects from any possible variations in symbioses in this study. Only minor differences were found in two provenances of *A. mangium* (inoculated with the same *Rhizobium* strain), except under high levels of P addition where one provenance declined in N fixation while the other increased (Sun et al. 1992). The range in seedling weights among 11 isolines of *L. leucocephala* was more than twofold (Sanginga et al. 1991) . Nitrogen-fixation rates of *C. equisetifolia* varied by twofold with respect to mg N-fixed $plant^{-1}$, whereas the range in %Ndfa ranged only from 50% to 80% (Sanginga et al. 1990). Variation in both measures of N fixation was much higher for *C. cunninghamiana*, ranging more than fivefold in mg N fixed $plant^{-1}$ and from 20% to 75% of percent N fixed. Galiana et al. (1990) examined several strains of *Rhizobium* and

Bradyrhizobium on single families of *Acacia mangium* and *A. auriculiformis*. Plant sizes spanned a 3-fold range among the inoculant treatments and N fixation plant^{-1} spanned a 10-fold range (among effective inoculant strains) for *A. mangium*, whereas the rate for the poorest inoculant on *A. auriculiformis* was more than half the rate of the best inoculant. Sougoufara et al. (1992) found that the ranking of *Casuarina* seedlings (based on seedling growth) was independent of the strain of *Frankia* inoculum. Similarly, the ranking of the *Frankia* strains (based on N fixation) was independent of the *Casuarina* clone. The genotype interaction in the symbiosis was not significant. In contrast, Mansour and Baker (1994) examined 4 *Casuarina* cultivars and 4 *Frankia* strains and found highly significant interactions between host and microbe strains. The salt-tolerance of *Casuarina* and *Frankia* strains was important in determining overall N-fixation rates; salt-tolerance of *Frankia* in vivo was a poor predictor of N-fixation performance under saline conditions (Girgis et al. 1992).

New techniques in microbiology and molecular biology are providing novel insights into the interactions between genotypes under plantation conditions (Sprent 1994). For example, Sanginga et al. (1994) examined the nodulation of a second-rotation plantation of *Leucaena leucocephala* in Egypt. The first-rotation seedlings had been inoculated with two highly-effective strains of *Rhizobia*. Serological typing of the nodules (using enzyme-linked-immunosorbent assays) in the second-generation *Leucaena* showed that 96% of the nodules derived from the *Rhizobia* strains inoculated 10 yr earlier on the first-generation trees.

Genetic selection in N-fixing symbioses can focus on a variety of features, including nodule mass, rate of N fixation per gram of nodule, total N fixation rate per plant and the percent of the plant's N derived from the atmosphere. Overall N fixation activity may differ among provenances, families and genotypes depending on the feature of selection. For example, a particular strain of *Rhizobium* (Strain 23c) produced only about half the nodule mass on *Acacia* as did some other strains, yet seedlings inoculated with this showed the greatest N fixation rate per plant (Galliana et al. 1990).

At present, the genotype symbioses cannot be optimised in operational plantations; the best course would probably be to minimise any use of inferior genotypes of host, N-fixing bacteria or mycorrhizae. The best operational approach to handling the genotypic diversity in nitrogen-fixing systems would be to: 1) select for a superior tree genotypes (for both growth rate and merchantability characteristics); and 2) inoculate nursery seedlings with strains of bacteria (and perhaps mycorrhizae) that have been shown to be highly effective.

Nutrient Cycling

The effects of N-fixing trees on ecosystem nutrient cycles depend on the amount of N fixed, the quantity of N and other nutrients taken up from the soil, the quantity and quality of litter input to the soil, any changes in soil microclimate and any changes in soil microflora and fauna. Field-based estimates of N fixation in tropical plantations are rare (Table 9.1), but rates of about 80 kg N ha^{-1} yr^{-1} for *Casuarina* and 100 to 150 kg N ha^{-1} yr^{-1} for tree legumes may represent average expectations. The Nfda typically ranges from about 50% to 80% across species, though the sensitivity of this fraction to age or to accretion of N over time remains largely unexamined under field conditions.

N-fixing trees typically take up greater quantities of nutrients from soils than non-N-fixers. For example, Binkley et al. (1992) found that aboveground litterfall in 6-yr-old plantations of *Albizia falcataria* cycled 6 times more N, 3 times more P and 2 times more Mg than 6-yr-old plantations of *Eucalyptus saligna* (see later discussion of this case study). The return of N in litterfall typically ranges from 130 to >200 kg N ha^{-1} yr^{-1} in tropical plantations of N-fixing trees (e.g. Sandhu et al. 1990; Binkley et al. 1992; Montagnini et al. 1993).

The decomposition rates of N-fixing litter are typically much higher than those for litter of other trees, although decomposition rates can vary substantially among N-fixing trees (cf. Sandhu et al. 1990; Bernhard-Reversat 1993; Montagnini et al. 1993; Mulongoy and Gasser 1993; Sankaran 1993; Sankaran et al. 1993; Mwiinga et al. 1994; Nyathi and Campbell 1994). N-fixer litter decomposes rapidly because of high nutrient contents and low contents of decay-resistant carbon compounds. Although the ratio of lignin:N predicts litter decomposition well in temperate forests (cf. Berg and McClaugherty 1987), variations in lignin in tropical forests appear much less important. The best indicator of decomposability of leguminous litter in tropical settings appears to be the polyphenolic content of the litter (Fox et al. 1990). Palm and Sanchez (1990) found that the polyphenolic content of 3 legume litters affected decomposition and nutrient release much more than did the concentrations of N or lignin. Palm and Sanchez (1991) also experimented with ground litter mixed into mineral soil and found that net N release correlated well with polyphenolic content ($r = -0.63$) or the ratio of polyphenol to N ($r = -0.75$).

Differences in litter chemistry may also dramatically affect the 'food' quality of litter for soil animals, which in turn may strongly affect nutrient turnover rates. Little information is available from tropical plantations, but the effects may be very large. Zou (1993) found 470 earthworms m^{-2} in plantations of *A. falcataria*, compared with only 90 m^{-2} in adjacent plantations of *E. saligna*. He estimated that the flux of N through earthworm tissues was about 150 kg N ha^{-1} yr^{-1} for the *Albizia* plantations, versus 30 kg N ha^{-1} yr^{-1} for the *Eucalyptus* plantations.

Soil changes under N-fixing trees

Soils in tropical forest plantations often show rapid changes in soil physical properties and chemistry, especially when trees are planted on old agricultural fields (Sanchez et al. 1985; DeBell et al. 1989). Few data are available on soil changes under N-fixing trees, but these probably include increases in total and available N and variable changes in other properties.

In a 34-yr, unreplicated age sequence of *Casuarina equisetifolia* in Senegal, the accumulation of nutrients in the forest floor was very large (1600 kg N ha^{-1} and 85 kg P ha^{-1}; Mailly and Margolis 1992). In this case, decomposition of *Casuarina* litter appeared inhibited by dry conditions and perhaps by P availability. Soil total P and exchangeable Ca declined across the age sequence.

An unreplicated comparison of stands of *Acacia auriculiformis* (5 yr old), *Pinus kesiya* (8 yr old), and grassland on Luzon in the Philippines found that *Acacia* improved structure and porosity in the surface 5 cm of mineral soil (Ohta 1990). *Acacia* also increased water conductivity of the soil, whereas *Pinus* reduced it (owing to hydrophobic mycelia of ectomycorrhizae). Soil nutrient contents (to a depth of 10 cm) appeared to decline under both tree species, including lower soil C, N, available P and Ca. The biomass and numbers of soil animals, particularly earthworms, appeared to be much higher under *Acacia* than in the grasslands or under the pines. Only net mineralisable N (aerobic incubations) appeared to have increased (by 50% to 100%) under the influence of either species.

Sankaran et al. (1993) compared soils under 23, 3-to-6-yr-old plantations of *A. auriculiformis* with adjacent fallow land to evaluate the effects of *Acacia* on soils. No significant differences were observed, except for a slight depression of the upper soil pH (from 5.0 under fallow conditions to 4.7 under *Acacia*).

Replicated 4-yr-old plantations of N-fixing *Stryphnodendron excelsum* (Fabaceae, Mimosoideae subgroup) in Costa Rica showed no substantial differences in soil C, N or P to three non-N-fixing, native tree species (Montagnini and Sancho 1994).

Soil N mineralisation (under laboratory conditions) in a natural forest of *Acacia seyal* was 4-times greater than under an 8-yr-old plantation of *Eucalyptus camaldulensis* (Bernhard-Reversat 1988). Higher N mineralisation in the acacia soils resulted from high net release of N from the large fraction (particles ~1mm) of the soil; about 5% of the N in this fraction was released from acacia soils, compared with 0% for eucalypt soils. Net mineralisation rates were high (about 7% of the total N released) from the very small fractions of the soil (particles <0.05 mm) for both soils.

Cortina and Binkley (unpublished) sampled soils under a species trial in Puerto Rico, where Wang et al. (1991) examined growth and nutrient content of vegetation. After 6 yr of species influence on the Vertisol soil, anaerobic incubations indicated greatest N availability (about 30 mg kg^{-1} dry soil) under two provenances of *Leucaena leucocephala* (Hawaiian K8 and a local variety), intermediate N availability (about 11 mg kg^{-1}) under *Casuarina equisetifolia* and *Cassia* (a non-N-fixing legume) and lowest (<5 mg kg^{-1}) under *Alibizia procera* (which did not grow well) and *Eucalyptus robusta*. All the N-fixers that grew well at this site appeared to increase N availability relative to *Eucalyptus*, but not equally well.

Tree species often induce changes in soil pH, including both acidification and alkalisation (Sanchez et al. 1985). Processes that could lead to soil acidification under N-fixing plantations include:

- accumulation of so-called base cations in biomass, which is matched by extrusion of H^+ from roots;
- accumulation of strongly-acidic soil organic matter; and
- loss of base cations from the soil profile in association with high leaching losses of nitrate anions.

In the northwestern US and southwestern Canada, intensive studies with N-fixing red alder have documented a full range of influences on soil pH (Van Miegroet et al. 1989; Binkley and Sollins 1990). Across the available studies, the impacts of alder have included: 1) no effect on soil pH or soil cations; 2) no change in pH but increased base saturation, indicating stronger organic matter acidity under alder; 3) lower pH as a result of no change in base cations, but decreased base saturation owing to accumulation of organic matter; and 4) lower pH from a combination of accumulation of strongly acidic organic matter and reduced base saturation from accelerated leaching losses of base cations.

Under more tropical conditions, Herbert (1984) reported on changes in surface soil pH through 3 rotations of *Acacia mearnsii* in South Africa; pH declined by 0.3 to 0.8 units after 2 rotations, but then increased by about 0.3 units after the third rotation. Rhoades and Binkley (1996) examined acidification under the influence of *Albizia falcataria* and *E. saligna* in Hawaii (see Case Study No. 2 below). After 8 yr, the pH of the 0–20 cm mineral soil declined from 5.9 to 4.6 under *Albizia* and to 5.0 under *Eucalyptus*. In both cases, soil acidification was driven by the accumulation of nutrient cations in biomass, with increasing aluminium saturation of the exchange complex. Nitrate leaching may have been important in the extra acidification under *Albizia*, but the difference in cation accumulation in biomass was more than sufficient to explain the difference in pH.

N supply to associated vegetation

Vegetation grown under the influence of N-fixing trees may enjoy an increased N supply. How large can this effect be? Only limited insights are available. For example, ^{15}N-labelled cuttings from *Leucaena leucocephala* were applied to a maize crop, and within 50 days more than half of the 42 kg N ha^{-1} applied in the cuttings had been released through decomposition (Xu et al. 1993). However, only 5% of the N applied in the cuttings was found within the maize crop; about 25% was found in the soil (with some as deep as 1 m) and 25% was apparently lost from the system. Application of N fertilizer (at a very low rate of 6 kg ha^{-1}) resulted in far higher N acquisition by maize, reaching about 50% in 50 days. P. Khanna and J. Raison (pers. comm.) established mixed plantations of *Eucalyptus globulus* and *Acacia mearnsii*; at age 2 yr the N concentrations in *Eucalyptus* leaves was very low in monoculture (10 mg g^{-1}) and significantly higher in mixtures with *Acacia* (up to 15 mg g^{-1}).

An elegant study by van Kessel et al. (1994) used changes in the natural abundance of ^{15}N to trace N fixed by *L. leucocephala*. The *Leucaena* obtained about 75% of its N supply (during the first 2 yr) from fixation. One yr after planting, the natural abundance of ^{15}N in understorey vegetation was about 7.3‰ higher than the ratio of N isotopes in the atmosphere, whereas the σ^{15}N of leaves and branches of *Leucaena* were 0.5 and 4.0‰ (Fig. 9.1). After 6 yr, the σ^{15}N of the understorey plants had declined to about 1‰. This decline in ^{15}N indicated that more of the understorey's N supply was derived from the atmosphere (via *Leucaena*) and less from the pre-existing soil N pools. By yr 6, the natural abundance of ^{15}N in *Leucaena* and the understorey plants was the same, indicating that the understorey received as high a proportion of its N supply from recently fixed N as did the *Leucaena*. The use of natural variations in ^{15}N abundance may have great potential for tracing recently-fixed N at sites where the initial ^{15}N abundance is substantially different from the atmosphere.

How does N move from N-fixing trees to associated vegetation? Most of the transfer is thought to result from normal nutrient cycling processes of litterfall (including both aboveground litter and root mortality), decomposition and changes in soil N supply (Baker 1990). However, under very controlled conditions it is possible to demonstrate a transfer of N between N-fixing and nonfixing plants via a common VA mycorrhiza (e.g. Haystead and Marriott 1979; van Kessel et al. 1985), or simply through exudation of N from roots. The ecological importance of such connections remains unknown. The potential importance appears to be large enough to warrant more work. For example, Rao and Giller (1993) 'fed' the leaves of 3-month-old *Leucaena* seedlings with ^{15}N and then looked for labelled N four weeks later in grass plants in the same pots. From 3% to 4% of the *Leucaena*'s N was transferred to the grass, accounting for about 30% of the grass's total N supply.

The pots were not inoculated with mycorrhizal fungi, so the mechanism of N transfer to the grass was unclear.

Nutrient limitations in N-fixing plantations

Many native tropical forests are expected to be limited by low supplies of P (especially on ancient soils) and N (cf. Vitousek and Sanford 1986). Virtually all pot studies with N-fixing tree seedlings have found substantial growth responses to added nutrients, especially P (studies cited above). Declining foliar nutrient levels with age have been reported for some situations (cf. Paudyal and Majid 1992), which suggest increasing nutrient limitation with stand age. Few field-based studies of nutrient limitations in N-fixing plantations exist, but those few have demonstrated very strong responses. For example, *Acacia mangium* planted on a site formerly occupied by imperata grass (FORTECH 1994) responded strongly to addition of P (with 18% better growth) and to further addition of N+K (7% better growth than +P alone). Dudley (1990) examined fertilisation responses of *Leucaena leucocephala* on a shallow, rocky site on the island of Hawaii. All trees received 80 kg N ha^{-1}, 35 kg P ha^{-1} and 65 kg K ha^{-1} at planting and 'fertilised' plots received the same doses at age 6, 12 and 18 months. The repeated fertilisation treatment increased accumulated biomass by more than 3-fold; however, this acidic site was not well suited for *Leucaena*, so the fertilisation response is difficult to extrapolate to suitable sites.

One of the best fertilisation studies in the literature happens to involve N-fixing *A. mearnsii*. The Wattle Research Institute in South Africa established a 3^4 factorial with this *Acacia* in 1948 with fertilisation treatments of 3 levels of each of N, P, K and lime in a Latin square design at 2 sites (Herbert 1984). The study continued through 3 rotations, with varying precipitation on a decadal scale. At Site 1 (Fig. 9.2), the first-rotation productivity showed no response to addition of P alone (at 37 kg ha^{-1}), but growth increased by 25% to P+K (K at 110 kg ha^{-1}). In the second rotation, the response to P alone became significant, but P+K still gave the better response. By the third rotation, P alone was responsible for most of the growth increase. Liming and addition of N gave little response. Note that the productivity differed substantially across rotations, probably as a result of differences in average precipitation during each rotation. At the second site, productivity was lower overall and the response to P alone was much greater than in the first site and showed no signs of change across rotations. This intricate study showed that fertilisation response by N-fixing trees may be substantial, and probably varies across sites. In addition, the growth response to fertilisation may change through time, as a result of factors such as precipitation variation or cumulative effects of management activities.

Combining the responsiveness of N-fixing seedlings in pot studies to fertilisation with the widespread responses to fertilisation observed for non-N-fixing trees leads to the conclusion that field plantations of N-fixing trees are likely to be nutrient limited. Indeed, it would be hard to imagine that the very high rates of growth reported for many N-fixing plantations could be sustained without supplemental fertilisation.

In conjunction with the *Albizia/Eucalyptus* case study presented later, several generalisations can be offered about nutrient cycling in N-fixing plantations:

- Nutrient uptake and subsequent cycling in litterfall are greater in plantations with N-fixing species;
- Nutrient recycling through decomposition is very rapid for high-quality litter from N-fixers, especially with adequate moisture; and
- Depletion of nutrient pools in mineral soils (in the absence of heavy fertilisation) may be substantial (especially if nutrient removal in biomass harvest is large), leading to creation (or exacerbation) of nutrient limitations on growth and N fixation.

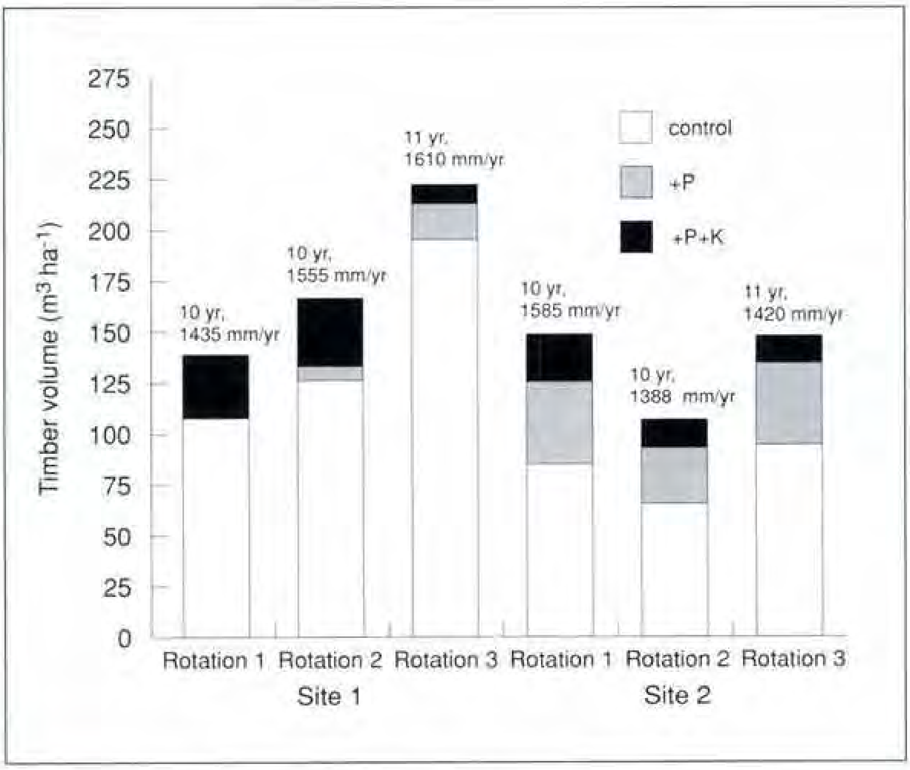

Figure 9.2 Volume accumulation by black wattle (*Acacia mearnsii*) at two locations in South Africa, across 3 rotations. Bars represent volume accumulation in the control plot, the additional volume resulting from addition of P alone (37 kg ha^{-1} once each rotation), or from addition of P plus K (112 kg ha^{-1} each rotation). Within each site, the productivity of each rotation (10 or 11 yr) tracked average annual precipitation at a decadal scale (from Herbert 1984)

Comparisons of Plantation Productivity

Much of the information available on the productivity of N-fixing trees comes in the form of height and diameter information from species trials. MacDicken (1994) provides a good summary of this information, including some basic information on precipitation and temperature for each site. A typical set of species trials was reported by Schubert and Whitesell (1985), testing a variety of species at five locations on Hawaii. In general, *Eucalyptus* species performed best (in terms of height and diameter growth), although *Albizia falcataria* and *Acacia mangium* were top performers in some cases. One trial included *Casuarina equisetifolia*, which did not grow well in the high (> 4000 mm yr^{-1}) rainfall environment. The authors noted that the effect of seed provenances within species may be as important as any differences among vigorous species.

Much less information is available for growth and yield in terms of volume or biomass (Table 9.2). Most case studies have been designed only for short-term results, and have not examined the processes behind differences in growth rates between species. As noted in Chapters 3 and 12, the biomass production of a plantation depends on:

- the supply and acquisition of resources (such as mass of nutrient uptake per hectare);
- efficiency of resource use (such as the mass of net primary productivity per mass of nutrient used); and
- allocation of photosynthate to various tissues such as roots and stems.

Differences between the productivity of N-fixing and non-N-fixing trees depend on the extra N supply (resource) available to the N-fixer and then any differences in: 1) the acquisition and efficiency of use of resources; and 2) the patterns of photosynthate allocation. N-fixing trees typically show lower N-use efficiency than non-N-fixing trees, as evidenced by higher concentrations of N in foliage and lower rates of wood production per kg of N used (Binkley et al. 1992). Fast-growing non-N-fixers, such as *Eucalyptus* species, may show higher use efficiencies for a variety of resources relative to N-fixers, so overall comparisons of growth between species may depend as heavily on resource use efficiency as on rates of N fixation (see Case Study No. 2 below).

A variety of growth studies have demonstrated rapid growth for N-fixing species. The overall productivities from these studies are summarised here, and two case studies (*Eucalyptus*, *Casuarina* and *Leucaena* in Puerto Rico and *Eucalyptus* and *Albizia* in Hawaii) are discussed in detail later.

Acacia auriculiformis produced much more biomass than either *Dipterocarpus turbinatus* or *Pinus caribaea* in a study in India, with proportionally greater accumulation of nutrients in *Acacia* biomass (Osman et al. 1992). Bhatnagar et al. (1993)

examined productivity of *Leucaena leucocephala* and *Acacia nilotica* in a tightly packed, hexagonally designed plantation. *Leucaena* achieved more than twice the height and 10 times the volume of *Acacia*, in both pure and mixed plantations.

Four indigenous tree species were compared in Costa Rica, including N-fixing *Stryphnodendron excelsum*. The N-fixer grew very well, averaging 8.8 t ha^{-1} yr^{-1} of stem increment over 4 yr; this was 16% less than the best of the non-N-fixers, but the difference in yield was not significant (Montagnini and Sancho 1994). Nitrogen-fixing *Stryphnodendron* accumulated more than 400 kg N ha^{-1} in biomass, more than double the amount of the non-N-fixing trees. No exotic species were included for comparisons in this study.

The productivity of pure stands of *Eucalyptus grandis* and *E. saligna* (which grew equally well) in Hawaii was compared with 50:50 mixtures of *Eucalyptus* with *Albizia falcataria* and *Eucalyptus* with *Acacia melanoxylon* (DeBell et al. 1985). At age 5.5, the pure *Eucalyptus* plots had 38 t ha^{-1} of total aboveground biomass, compared with 52 t ha^{-1} for the *Eucalyptus/Acacia* mixtures and 95 t ha^{-1} for the *Eucalyptus/Albizia* mixtures. Plots with *Acacia* had as much *Eucalyptus* biomass (on bigger stems) as the pure *Eucalyptus* plots and the plots with *Albizia* had 50% more *Eucalyptus* biomass (on very large stems!).

The 2-yr growth of several species on a wet (4700 mm rain yr^{-1}) Histosol soil on Hawaii (Dudley 1990) showed poor growth for *Leucaena leucocephala*, whereas *Acacia mearnsii* grew about as well as several *Eucalyptus* species (Table 9.2). In a broader comparison of species, MacDicken and Brewbaker (1989) reported on 2-yr growth of five legume tree species from five sites in Hawaii and in the Philippines. Plantations were planted very densely (1 × 1 m) and two sites in Hawaii received irrigation water. Across all sites, the greatest average wood volume increments were found for *Leucaeana leucocephala* and *L. diversifolia* (about 47 m^3 ha^{-1} yr^{-1}), followed by *Sesbania grandiflora* (38 m^3 ha^{-1} yr^{-1}). *Calliandra calothyrsus* and *Acacia auriculiformis* did not grow well across these sites (12.5 m^3 ha^{-1} yr^{-1}). Any extrapolation of 2-yr results from high density plantations to normal plantation practices and rotation lengths is problematic.

A very thorough study in Indonesia is comparing the silviculture and growth of six species of *Acacia* with a wide range of *Eucalyptus* species and hybrids on former *Imperata* grasslands (FORTECH 1994). *A. mangium* grew particularly well compared to the *Eucalyptus* species, accumulating up to 56 m^3 ha^{-1} of wood at 30 months of age. Application of glyphosate herbicides doubled *Acacia* biomass at 30 months, whereas physical cultivation (harrowing or ploughing) had no substantial effect. A variety of silvicultural factors influenced the growth of *A. mangium* through 30 months; provenance accounted for about 40% of the total variation in growth, compared with 35% for weed control, 18% for P fertilisation and 7% for N+K fertilisation.

Table 9.2 Comparisons of aboveground biomass and increment for N-fixing and non-N-fixing tropical plantations

Location	Species, age, treatment	Biomass (t ha^{-1})	Current increment (t ha^{-1} yr^{-1})	Reference
Hawaii	*Albizia falcataria*, 4 yr, fertilised at planting and every 6 months till 48 months	110 total age 4		DeBell et al. 1989
		131 total age 6	20 wood age 6	Binkley et al. 1992[a]
		200 total age 10		DeBell et al. 1997
	Eucalyptus saligna, 4 yr, fertilised at planting and every 6 months	94 total age 4		
		134 total age 6	20 wood age 6	
		170 total age 10		
	0.66 *Albizia*/0.34 *Eucalyptus*, 4 yr, fertilized at planting	51 total *Albizia* age 4		
		53 total *Eucalyptus* age 4		
		50 total *Albizia* age 6	5 wood *Albizia* age 6	
		104 total *Eucalyptus* age 6	30 wood *Eucalyptus* age 6	
		66 total *Albizia* age 10		
		184 total *Eucalyptus* age 10		
Hawaii	*Acacia mearnsii*, 2 yr, fertilised at planting and every 6 months	41 total	20	Dudley 1990
	Eucalyptus grandis, 2 yr, fertilised at planting and every 6 months	46 total	23	
Hawaii	*E. grandis/saligna*, 5.5 yr, fertilised at planting and at 15 months	38 total		DeBell et al. 1985
	1:1 mix of *E. grandis/saligna* with *Albizia falcataria*	37 total *Albizia* 58 total *Eucalyptus*		
	1:1 mix of *E. grandis/saligna* with *Acacia melanoxylon*	16 total *Acacia* 35 total *Eucalyptus*		
Puerto Rico	*Casuarina equisetifolia*, 5.5 yr	199 total; 143 wood		Wang et al. 1991
	Albizia procera, 5.5 yr	124 total; 101 wood		
	Leuceana leucocephala K8 var., 5.5 yr	47 total; 37 wood		
	L. leucocephala, PR var., 5.5 yr	33 total; 24 wood		

Table 9.2 (cont'd) Comparisons of aboveground biomass and increment for N-fixing and non-N-fixing tropical plantations

Location	Species, age, treatment	Biomass (t ha^{-1})	Current increment (t ha^{-1} yr^{-1})	Reference
Puerto Rico	*Eucalyptus robusta*, 5.5 yr	67 total; 45 wood		
	Casuarina equisetifolia, 4 yr	105 total		J.A. Parrotta, pers. comm.
	Eucalyptus x *robusta*, 4 yr	63 total		
	Leucaena leucocephala, 4 yr	72 total		
	Casuarina/Eucalyptus, 4 yr	69 *Casuarina* total 27 *Eucalyptus* total		
	Casuarina/Leucaena, 4 yr	90 *Casuarina* total 34 *Leucaena* total		
	Eucalyptus/Leucaena, 4 yr	31 *Eucalyptus* 69 *Leucaena*		
Bangladesh	*Acacia auriculiformis*, 4 yr	76 total; 58 wood		Osman et al. 1992
	Dipterocarpus turbinatus, 8 yr	32 total; 23 wood		
	Pinus caribaea, 4 yr	62 total; 29 wood		
Costa Rica	*Stryphnodendron excelsum* (N-fixer) 4 yr no fertilisation	35.3 stem 54.8 total		Montagnini and Sancho 1994
	Vochysia ferruginea, 4 yr no fertilisation	24.8 stem 44.9 total		
	Vochysia hondurensis, 4 yr no fertilisation	41.8 stem 55.5 total		
	Hyeronima alchorneoides, 4 yr, no fertilisation	26.3 stem 43.9 total		

[a] 6-yr data revised from Binkley et al. 1992, revised with better *Eucalyptus* biomass regression equations (D. DeBell, pers. comm.)

Sustainability of plantation productivity

The long-term sustainability of high productivity in tropical plantations depends in part on a continued supply of nutrients. Rapid growth of tropical plantations leads to high rates of nutrient accumulation in biomass, and harvesting at short rotation intervals removes large quantities of nutrients and may deplete soil fertility. The long-term sustainability of soil fertility under the influence of rapidly-growing trees is not well known, but large removals of nutrients in harvested biomass of N-fixing trees must deplete soil pools. The significance of this depletion depends on tree rooting depths, rates of mineral weathering and fertilisation (see Sanchez et al. 1985).

The sustainability of soil fertility under the influence of N-fixing trees may differ from other cases. The addition of N to the soil may partially or fully offset N removals in harvest. However, rapid biomass production coupled with high nutrient concentrations in the biomass of N-fixing trees could accelerate the removals of other nutrients such as P, Ca and K. The type of biomass harvested also has a large effect on nutrient removal (see Chapter 12). For example, Montagnini and Sancho (1994) estimated that whole-tree harvesting of N-fixing *Stryphnodendron excelsum* would remove about 400 kg N ha^{-1}, compared with just 180 kg N ha^{-1} in a stem-only removal. The differences between whole-tree and stem-only removals were more accentuated for Mg than N, but were much smaller for Ca than for N. Short-rotation harvesting may remove more nutrients than longer-term rotations (both in terms of kg lost ha^{-1} yr^{-1} and kg lost per kg of wood harvested), because of a higher proportion of nutrient-rich bark and sapwood in smaller trees as well as other factors.

Some authors have suggested that nutrient ions found deep within soil profiles may be tapped by deep-rooting trees, with subsequent recycling in the upper soil, but the evidence is weak (Sanchez et al. 1985). Alternatively, deep leaching of nutrient ions, either during normal stand growth periods or after harvesting, may result in substantial nutrient losses. Unfortunately, these possible sources and losses of nutrients remain largely unknown and warrant much more research. Leaching losses of nitrate from N-fixing stands should have a high priority for research.

The selection of the most productive species or mixture of species depends heavily on the time frame of interest. The relative productivities of N-fixing and non-N-fixing species depends upon rotation length (rapid early growth may not indicate superior biomass at the end of a long rotation) and number of rotations of interest (rapid growth in the first rotation may not be matched by subsequent rotations). We can speculate that a fast-growing species that accumulates large quantities of nutrients may lead to lower productivity in a second rotation, but definitive information is not available. Similarly, a somewhat slower-growing, less-nutrient demanding species may have a higher level of productivity over a longer time span. Multiple-rotation research projects that examine the processes underlying changes in productivity are sorely needed.

Case Studies

Many studies have examined a few of the processes and patterns that result in the overall growth performance of tropical N-fixing plantations. The growth of a plantation depends on a range of interacting processes, and limited studies can provide only limited insights. Two case studies have provided the most complete picture of the ecosystem-level interactions that influence the productivities of N-fixing plantations in tropical environments. We present these two case studies in some detail, as they illustrate key interactions that may occur in other situations, and provide good templates for the design of future studies.

Casuarina, *Leucaena* and *Eucalyptus* in Puerto Rico

Parrotta, Baker and Fried (1994a) established an intensive study to look at the productivity, N fixation and soil nutrient effects of three tree species: *Casuarina equisetifolia*, *Leucaena leucocephala* and *Eucalyptus robusta*. The experimental plantations were established at the Toa Baja experimental farm of the University of Puerto Rico, with a warm annual climate (29°C and 24°C average daily temperatures for August and January), moderate annual precipitation (1600 mm, with a moderately seasonal distribution) and alkaline (pH 8-8.4), sandy soils of marine origin. Before this study, the site had been used for a varied series of agricultural crops and pasture. The study design included 3 replicate plots (16 × 16 m) for each treatment and the treatments included pure plots of each species and 1:1 mixtures of each pair of species. Soil ^{15}N enrichment of subplots was used to estimate N fixation rates. Within each plot, a subplot (either 3 × 3 m or 4 × 4 m) was trenched and lined with a plastic barrier to restrict root growth across subplot boundaries. Two additional untrenched subplots were established in each plot. Every 6 months, the trenched and untrenched subplots received the equivalent of 10 kg N ha^{-1} as ^{15}N-labelled ammonium sulfate. The remaining area of each plot received the same amount of unlabelled fertilizer. Sampling of leaf and woody tissues for N content and ^{15}N concentrations allowed the contribution of soil N to be separated from the contribution of atmospheric N. Up to age 3.5 yr, *Casuarina* trees fixed about 60% of their N in monocultures and mixtures with *Eucalyptus* or *Leucaena* (Parrotta et al. 1994b; J. Parrotta pers. comm.). *Leucaena* fixed more than 90% of their N at age 2.0 yr in monoculture, declining to about 40% by age 3.5 yr (Parrotta et al. 1994b; J. Parrotta, pers. comm.). However, the decline in contribution of N fixation to *Leucaena*'s N supply resulted from a dramatic increase in N use rather than a decline in N fixation ha^{-1} yr^{-1}; annual fixation rates for both *Casuarina* and *Leucaena* were about 70 to 75 kg N ha^{-1} yr^{-1} both at age 2 and 3.5 yr. At age 2 yr, *Eucalyptus* from either the monocultures or from the mixtures served equally well as non-N-fixing 'controls' to sample the isotope ratio of soil N. Recently-fixed N entered the available N pool in the soil in plots containing N-fixing trees by age 3.5, lowering the ^{15}N enrichment of *Eucalyptus* in the mixed plots. Therefore, use of the isotope abundance of N in the *Eucalyptus* monoculture (rather than from the mixture) would have provided a biased estimate of the labelling of the soil N pool.

After 4 yr, the *Eucalyptus* monoculture had the lowest aboveground biomass (about 65 t ha^{-1}, Fig. 9.3, from information provided by J. Parrotta). The mixture of *Casuarina* and *Leucaena* had the greatest biomass (about 125 t ha^{-1}), but this was not significantly greater than the *Casuarina* monoculture (105 t ha^{-1}). The degree of ecological divergence between species can be calculated as the relative yield totals of mixtures. The biomass of each species in mixture is divided by the biomass of that species in monoculture and the two values are summed. For example, the *Eucalyptus* in the mixture with *Leucaena* produced half as much biomass as in monoculture plots, but the *Leucaena* produced 96% as much biomass in the mixtures as in monoculture plots. Summing these two provide a relative yield total of 146% for this mixture. The relative yield total for the *Casuarina/Eucalyptus* mixture was 109% and that of the *Casuarina/Leucaena* mixture was 133%.

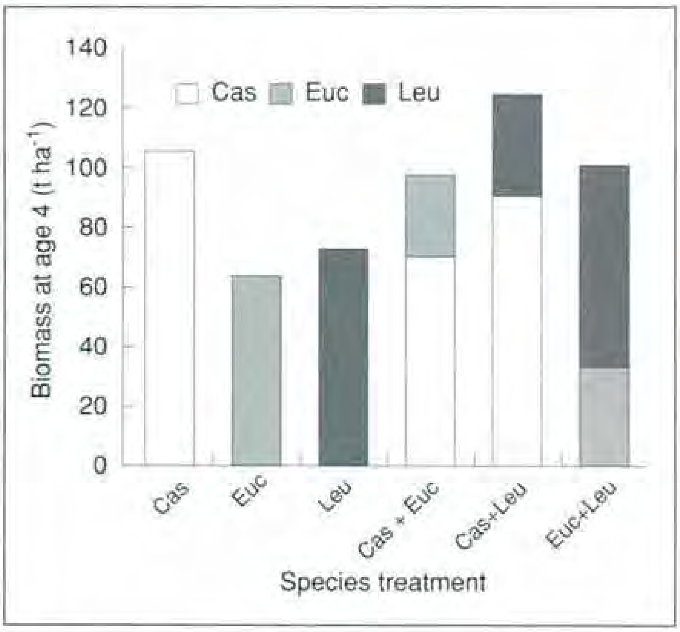

Figure 9.3 Aboveground biomass in monoculture and mixtures at age 4 yr; Cas = *Casuarina equisetifolia*, Euc = *Eucalyptus robusta* hybrid, Leu = *Leucaena leucocephala* (data from J. Parrotta, pers. comm.)

Soil N availability, as indexed by 21-day on-site incubations of 0–30 cm depth soil in plastic bags, showed very high variation across plots (J. Parrotta, pers. comm.). Nitrogen availability appeared to be depressed in the *Casuarina/Leucaena* mixture (about 5 mg N released per kg of dry soil) compared with either monoculture (about 17 mg N kg^{-1}). These N mineralisation rates reflect the combined effect of each species on the gross release of N from organic pools and the immobilisation of N into microbial biomass. The lower net mineralisation values in the mixture may have resulted from either lower release of N in decomposition, or greater microbial uptake and storage of N.

This case study demonstrated that ^{15}N techniques can provide detailed estimates of N fixation rates through stand development, and show how N-fixation in mixed species stands may differ from monocultures. In addition, the case study shows that benefits of improved N nutrition of *Eucalyptus* may have been offset by competition for other resources (perhaps water?).

Albizia and *Eucalyptus* in Hawaii

Earlier studies in Hawaii showed strong N limitations on *Eucalyptus* productivity, so a series of research plantations were established to test the ability of *Albizia* to supply N to *Eucalyptus* (DeBell et al. 1989; Binkley et al. 1992; DeBell et al. 1997). A replicated block design was used to examine treatments of pure *Eucalyptus* (including supplemental N fertilization), pure *Albizia* and 5 ratios of mixtures. The experimental plantations were established on a deep (>2 m), acidic (pH 5.0), volcanic-ash soil (Typic Hydrand) with a moderate year-round climate (20°C and 23°C mean daily temperatures in January and August), high rainfall regime (4600 mm yr^{-1}, no seasonal dry period). Before this study, the site had been cropped with sugarcane for more than 50 yr, including repeated liming and fertilisation. In addition to this mixture experiment, replicated pure plantations of each species were established at two nearby locations. Rapid early growth of *Albizia* led to greater biomass accumulation at age 4 yr than in any other treatment (Table 9.1). *Eucalyptus* in plots with 66% *Albizia* were 20% taller and had 50% greater diameters than *Eucalyptus* in pure plots. By age 6, the 34% *Eucalyptus* / 66% *Albizia* plots had the greatest total biomass, with a current rate of biomass increment that was 50% greater than the pure *Eucalyptus* plots (which had received supplemental N fertilisation) and 90% greater than the pure *Albizia* treatment. The relative yield total was 120% in the 34% *Eucalyptus*/66% *Albizia* plots compared to the monocultures. By age 10 yr, the 34% *Eucalyptus*/66% *Albizia* plots had not only the greatest total biomass and increment rates, but also the greatest values for *Eucalyptus* biomass and increment (DeBell et al. 1997). The fertilised *Eucalyptus* trees (without *Albizia*) had lower N concentrations in foliage than those grown with a high ratio of *Albizia*:*Eucalyptus*. At age 4, the pure *Eucalyptus* trees had 1.8% N, compared with 2.1% N for *Eucalyptus* trees grown with 66% *Albizia*. More impressive was the increase in P concentrations: 0.16% in pure stands and 0.22% in 66% *Albizia* stands.

The patterns of productivity derived from interactions between resource supply (or acquisition) and the efficiency of resource use. For example, the canopies were stratified in height, with *Eucalyptus* canopies emerging above *Albizia* canopies (Fig. 9.4). Pure *Eucalyptus* canopies intercepted about 66% of incoming radiation, compared with 88% for the pure *Albizia* canopies. The stratified canopy of the 33% *Eucalyptus*/66% *Albizia* plots raised light interception to 92%. Dividing the energy content of aboveground net primary production by the annual interception of light provides estimates of light use efficiency: 16.8 kJ MJ^{-1} *Eucalyptus*, 14.0 kJ MJ^{-1} *Albizia* and 18.2 kJ MJ^{-1} for the *Eucalyptus/Albizia* mixture. The mixed plots had 53% greater aboveground net primary production than the pure *Eucalyptus* plots (52 t ha^{-1} yr^{-1} vs. 34 t ha^{-1} yr^{-1}) and this derived from a combination of 39% more light interception and 8% greater light use efficiency. Similar calculations for nutrient use efficiency showed that the overall pattern in productivity depended on the higher nutrient supplies under the influence of *Albizia* and the greater nutrient use efficiency of *Eucalyptus* (Binkley et al. 1992). Whole-tree harvesting of the pure *Albizia* plots would remove about 400 kg Ca ha^{-1} and 60 kg t ha^{-1}, compared with 320 kg Ca ha^{-1} and 36 kg t ha^{-1} for the pure *Eucalyptus* plots.

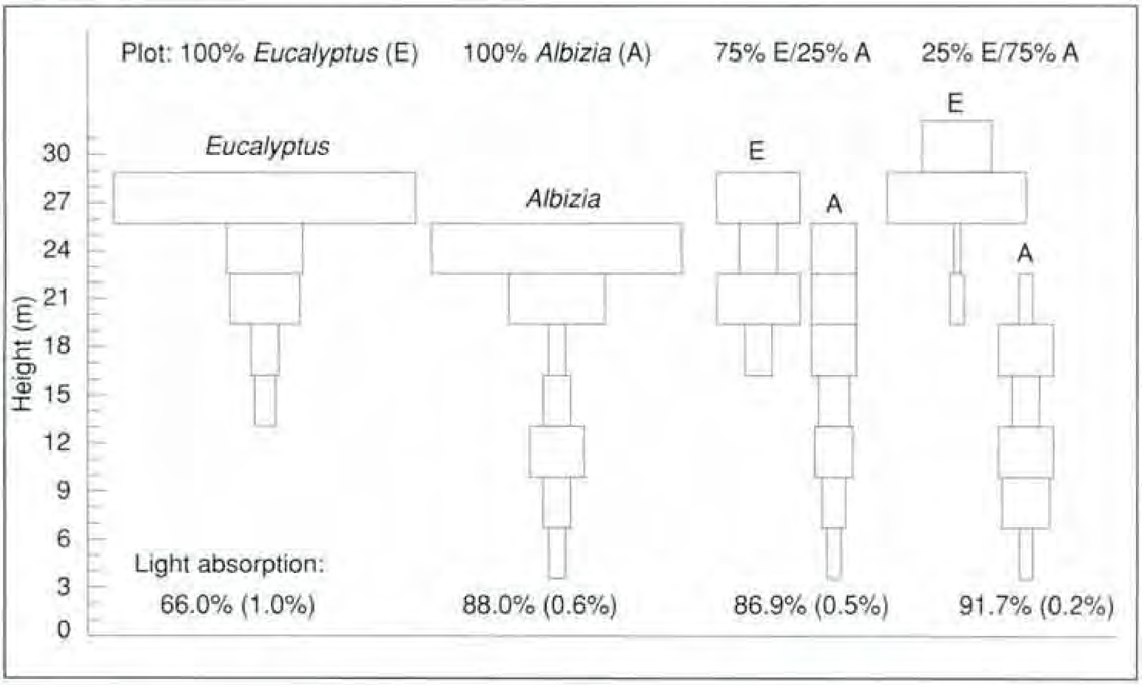

Figure 9.4 Canopy profiles and light interception for *Albizia falcataria* and *Eucalyptus saligna* plots in Hawaii (from Binkley 1992). (Standard errors are in brackets)

After 4 yr, the 0–20 cm mineral soil under the pure *Albizia* plots showed a 14% increase in total N, a decline in pH (from 5.9 initially to 5.2) and substantial declines in extractable calcium (from an initial 15 mmol$_c$ kg^{-1} to 1.1 mmol$_c$ kg^{-1}). The pure *Eucalyptus* plots showed no increase in N concentration, a more modest pH decline (to 5.4) and a similar decline in extractable Ca. A resampling at age 8

(Rhoades and Binkley 1996) showed a continued trend of declining pH (to 4.6 in pure *Albizia* and 5.0 in pure *Eucalyptus*). The *Albizia* plots at age 8 showed much higher exchangeable acidity (4.7 mmol$_c$ kg^{-1} vs. 1.5 mmol$_c$ kg^{-1} for *Eucalyptus*) and lower base saturation (35% vs. 46% for *Eucalyptus*). Soil acidification was driven by the accumulation of nutrient cations in biomass; the *Eucalyptus* plots contained about 40 kmol$_c$ ha^{-1} of nutrient cations in biomass, compared with 76 kmol$_c$ ha^{-1} in the *Albizia* plots. At age 8, the nutrient cation content of biomass was far greater than the extractable nutrient cations in the soil (to a depth of 0.7 m), so continued productivity of these plots would likely depend on cation resupply rates from mineral weathering or from fertilisation.

As found for other ecosystems with N-fixing trees, the return of N in aboveground litterfall exceeded 200 kg N ha^{-1} yr^{-1} for *Albizia* plots (240 kg N ha^{-1} yr^{-1} at age 6 yr; Binkley et al. 1992). Mixed plots had about 130 kg N ha^{-1} yr^{-1}, compared with just 40 kg N ha^{-1} yr^{-1} in pure *Eucalyptus* plots. The pattern of P in litterfall matched that of N, with 9.6 kg P ha^{-1} yr^{-1} in the pure *Albizia* plots, 6.0 kg P ha^{-1} yr^{-1} in the mixed plots and 3.0 kg P ha^{-1} yr^{-1} in the pure *Eucalyptus* plots. The N concentration of *Albizia* litter (2.3%) was far greater than that of *Eucalyptus* litter (0.9%) and the polyphenol concentrations were much lower (12 mg g^{-1}*Albizia*, 64 mg g^{-1} *Eucalyptus*). Simulations of litter decomposition rate suggested that *Eucalyptus* litter would take several times as long to decompose as *Albizia* litter.

As noted above, the differences in litter quality led to much greater earthworm densities under *Albizia* (470 m^{-2} vs. 90 m^{-2} for *Eucalyptus*; Zou 1993). The microbial communities also differed dramatically. Total bacterial biomass was 30% greater with *Albizia*, whereas active fungal biomass was twice as high under *Eucalyptus*; the ratio of fungal to bacterial biomass was 0.58:1 for *Albizia* and 1.34:1 for *Eucalyptus*. These differences in the soil communities were associated with twice as much phosphatase (the exoenzymes responsible for releasing P from organic compounds) activity in the *Albizia* soils than in the *Eucalyptus* soils (Zou et al. 1995). The implications of such large changes in the soil fauna and microflora remain largely unknown; are the changes merely effects of the trees, or are the effects of the trees dependent heavily on the changes in the communities? Would the patterns of nutrient cycling and growth have been the same in the absence of the exotic earthworms?

After 12 yr of plantation development we intensively characterised the soils under the pure species plots in the original mixture trial and in the 2 other species trials of the same age, on similar (but more fertile soils) within 2 km of the mixture trials (Binkley, Garcia and Giardina, unpublished). The overall experimental design provided 4 replicates for each species, at each of 3 sites. Soil C was marginally higher under *Albizia*, whereas soil N was about 25% higher (Fig. 9.5). Accretion of N in the upper 15 cm of soils averaged about 95 kg ha^{-1} yr^{-1} for 12 yr across all 3 sites. Accretion was significantly greater at the poorest of the three sites, averaging 140 kg ha^{-1} yr^{-1}, compared with 65 to 70 kg ha^{-1} yr^{-1} on the two richer sites. We do not know if the greater accretion at the poorest site derived from greater N fixation, less loss of fixed N (from leaching or denitrification), or from a different pattern of distribution within the ecosystem. Nitrogen mineralisation during anaerobic incubations was about 15% greater with *Albizia*; interestingly, ^{15}N tracer studies showed that the higher net mineralisation patterns resulted from greater immobilisation of N in *Eucalyptus* soils, rather than from greater gross mineralisation under *Albizia*. Available P (and other pools) appeared substantially lower in *Albizia* soils and this was confirmed in a bioassay experiment using *Eucalyptus* and *Albizia* seedlings (Fig. 9.6). *Albizia* seedlings were much larger when grown on *Eucalyptus* soils and they responded strongly to P (but not N) fertilization in both soil types. *Eucalyptus* seedlings, in contrast, grew much larger (40% more biomass) on *Albizia* soils and responded strongly to both P and N. The response of *Eucalyptus* seedlings to P fertilisation was greater in *Albizia* soils, also supporting the pattern of lower P supply in *Albizia* soils.

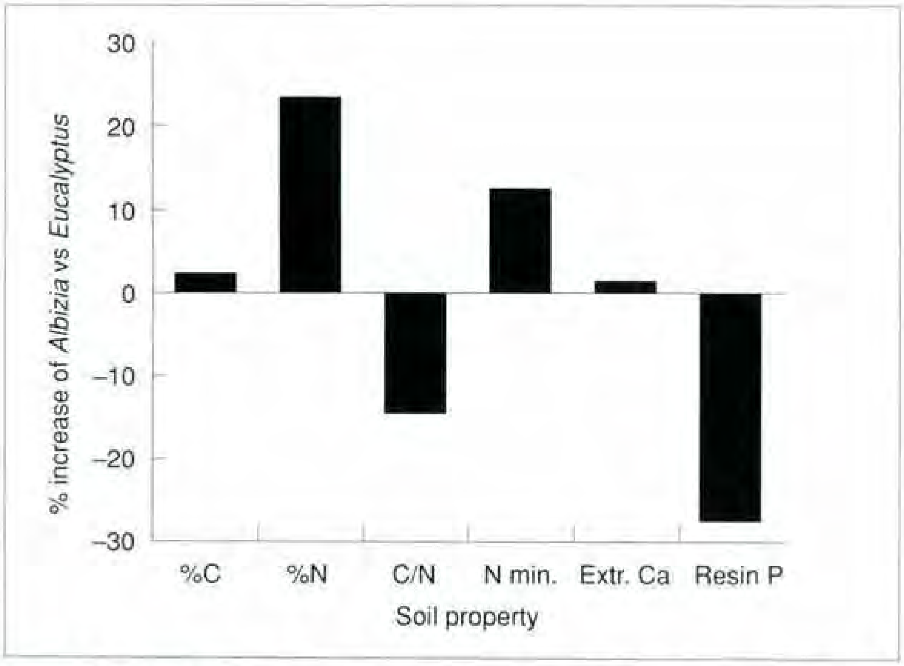

Figure 9.5 Differences in soil properties after 12 yr of influence of *Albizia falcataria* or *Eucalyptus saligna* (D. Binkley, D. Garcia and C. Giardina, unpublished data)

Overall, these Hawaiian plantations showed greatest growth and biomass accumulation in mixed stands; substantial increases in total and available soil N under *Albizia*; significant declines in soil P pools under *Albizia* and increased cycling of N and P in litterfall in stands with *Albizia*. Although *Albizia* decreased the supply of P in the soil, *Albizia* stands still obtained and cycled more P than *Eucalyptus* stands.

The well-replicated (both within and across sites) experimental designs in these case studies allowed for tests of the effects of species, block, site and interactions. The species effects were strong for most variables and the site effects were significant in some cases. Interestingly, block effects and all interactions were not significant, indicating no major interactions of the species effects across the sites examined.

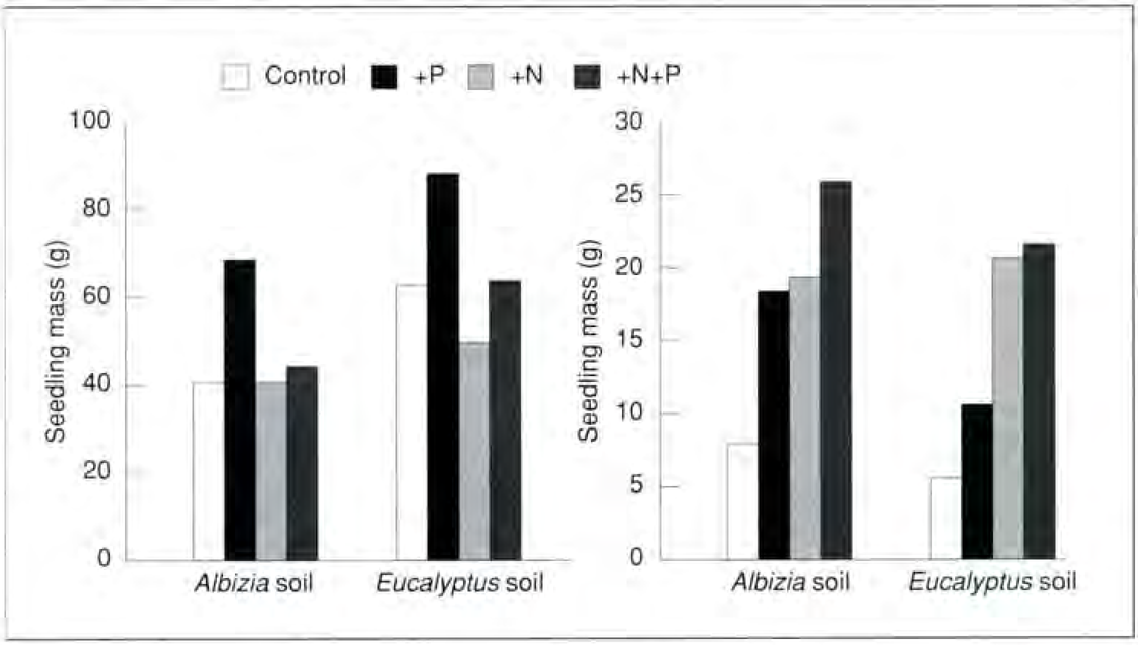

Figure 9.6 Bioassay of *Albizia* and *Eucalyptus* seedlings in soils from *Albizia falcataria* and *Eucalyptus saligna* plantations; *Albizia* seedlings grew better on *Eucalyptus* soils, and *Eucalyptus* seedlings grew better on *Albizia* soils (Binkley 1997)

Synthesis

The use and value of N-fixing trees always depends on a wide range of factors for each situation. Some of the factors are biological and ecological (How well will a species grow? How much N will be fixed?), but the most important issues are typically social (What type of wood is in demand in the local market? What are the objectives of the landowners?). Given the genetic diversity of N-fixing trees, species and provenances are available for almost any environment, from *Casuarina* and *Acacia* for semi-arid, high salinity situations, to *Albizia* for fertile soils with high rainfall. For most environmental settings, non-N-fixing tree species may also give acceptable growth rates and product values, so the decision of whether to use N-fixing trees will depend on the relative long-term productivity of the N-fixer, ease of management and the local market and social needs of the people.

Should indigenous species be used in preference to fast-growing exotic species? As noted in the studies by Montagnini et al. (1993) and Montagnini and Sancho

(1994), indigenous N-fixing species may be available that are well adapted to local environments. Well-informed choices between indigenous and exotic species are elusive, given the current lack of information (especially on features other than biomass production) on indigenous species and lack of comparison in well-designed studies with exotic species.

What might be the benefits and costs of using N-fixing trees to enrich soils, or to increase growth of interplanted non-N-fixers? Too few case studies are available to answer these questions, but some tentative insights are available. The Hawaii case study described above showed that mixed-species stands may indeed outperform monocultures. However, we also note that two out of three other attempts with mixtures on the on the same island failed; one site was too dry and windy for *Albizia* and *Albizia* totally suppressed *Eucalyptus* at the other. Mixed-species plantations will always present silvicultural challenges and risks relative to monocultures and they may be most suited for small-scale operations where stand tending operations (such as lopping of canopies or thinning out stems to manage the balance of competition) can ensure successful growth of each species. The Hawaii case study also showed that although *Albizia* increased soil N supply, it apparently decreased the P supply. If the existing plots were harvested and a second generation of *Eucalyptus* were planted, how long would the legacy of the previous species last?

The information needs of small landowners may differ substantially from those of industrial plantation managers. For small landowners, sustained soil fertility with minimal fertilisation may be a high priority. Industrial plantations may be able to afford investments in optimal levels of fertilisation. Research on both management approaches is vital.

Many of the studies currently available used very small plot sizes (100 to 600 m^2); these may be sufficient for short-term evaluations of site suitability of species, but they are generally too small to address longer-term questions, such as productivity of second-rotation stands. Future studies may benefit from including at least a subset of treatments in larger plots (at least 1000 m^2) that will facilitate insights into longer-term issues.

We have not addressed the economics of plantation establishment, optimal ratios of species in mixtures, tending, harvesting and marketing; these will all differ between species and silvicultural approaches and will play a very large role in determining the ultimate value of tropical plantations. Although such a discussion is beyond the scope of this chapter, we stress that the long-term sustainability of productivity must figure heavily in such evaluations. Rapid growth for the first 5 yr of the first rotation provides great information on establishment and survival (key issues in any plantation operation), but the long-term, sustainable level of production may be difficult to project with short-term information.

We have also not discussed insect and disease problems (which should be similar to non-N-fixing tree plantations), or the need for weed control in tropical plantations. Rapid growth in short-rotation plantations often depends on effective control of competing vegetation. In addition, minimising the competing vegetation may lead to earlier crown closure, greater recovery of fertilizer by crop trees and earlier maximisation of growth. Little information is available on the value of weed control for N-fixing vs. non-N-fixing plantations, although we do note that extensive use is made of *Leucaena leucocephala* to control weeds in plantations of teak and other high-value species (Seorianegara and Lemmens 1993). Great opportunities are available for creative silvicultural approaches to weed control in tropical plantations, especially where intensive stand tending is practical.

Research needs

The first research need is simply for more and better silvicultural knowledge of the major N-fixing species currently in use. Site-appropriate information is needed on potential yields and responses to silvicultural factors such as nursery management, provenance and genetic selection, spacing, pruning, harvesting and regeneration. Experience from a species at one location provides a guide for use of that species at other locations, but many local details (such as interactions of climate and soil) can be very important. Additional research into improving the symbioses between trees, N-fixing bacteria and mycorrhizal fungi may also improve the long-term performance of N-fixing trees. The current state of knowledge of these interactions is sufficient, however, for foresters to go ahead with operational plantations.

Perhaps the greatest need for research in the near future is on the role of nutrient limitation in the growth of N-fixing plantations and in sustaining soil fertility through a combination of N-fixation and fertilisation. Tropical plantations produce the greatest amount of wood per hectare of any forests and such high productivity clearly cannot be sustained after harvest of nutrient-rich biomass without specific attention to nutrition management. N-fixing trees are excellent exploiters of soil nutrient supplies; they even obtain 25% to 50% (or more) of their annual supply of N from the soils rather than expend resources to fix their entire supply. If N-fixing trees are harvested, how large will N removal be relative to the cumulative amount of N fixed during the rotation? If annual rates of N fixation are on the order of 75 to 125 kg N ha^{-1} yr^{-1}, and the N removed in harvest is typically 500 kg N ha^{-1}, most N-fixing plantations in the tropics probably range from little change in ecosystem N content, to moderate increases.

Many management decisions are based on patterns in stand productivity over time, with harvest intervals designed to obtain maximum yield of a product (such as stemwood) or economic return. We stress, however, that rapid changes in soil nutrient supplies may dominate any pattern of stand growth with age. Especially in situations where fertilisation is used at planting, declines in productivity with stand age may simply reflect declining soil fertility rather than an age-related decline in growth. Studies of nutrient limitation are clearly needed to separate manageable changes in growth rates from those that are less manageable (i.e. age-related). We know of no plantation studies with high-productivity N-fixing trees in the tropics that have yet been able to document the sustainability of productivity into a second rotation; and a great deal of first-rotation information indicates soil fertility is unlikely to be sustained without fertilisation. Appropriate nutrition management, such as fertilisation with P, may not only sustain or increase growth rates, it may also lead to higher rates of N fixation and improved soil fertility.

The third major research need is basic information on the potential and limitations of the many N-fixing trees that have not been explored or 'domesticated' for plantation use (see Leakey and Newton 1994 for background and details). *Acacia mangium* has been widely used in plantations for only 20 yr (National Research Council 1983) and its development started when an Australian forester thought the species might grow well in Malaysia. Many other species are awaiting testing, from within the genera commonly in use and from genera receiving less interest such as *Sesbania* (currently used mostly in agroforestry situations), *Gliricidia sepium* (Parrotta 1992b), *Parasponia* species (Domingo 1983) and *Dalbergia* and *Pithecellobium* species (Parrotta 1989, 1991). In addition, some non-N-fixing trees, such as leguminous *Cassia*, may improve soil N supplies as well or better than N-fixers (c.f. Garrity and Mercado 1994), and these possibilities (and mechanisms) need to be explored. We also note that species of *Alnus* may be well suited for certain conditions in tropical regions, including *Alnus jorullensis* in South America (e.g. Carlson and Dawson 1985) and *Alnus nepalensis* in Asia (e.g. Sharma 1988; Sharma and Ambasht 1988).

Acknowledgments

The writing of this review was supported in part by NSF grant No. DEB93-06356 and by McIntire Stennis appropriations to Colorado State University. We thank Dwight Baker, John Parrotta, John Turnbull, Peter Högberg, Cheryl Palm, Chuck Rhoades, Michael Bashkin, Florencia Montagnini, Mark Paschke, Y.R. Dommergues and the workshop participants for helping us improve this chapter and John Parrotta and Dwight Baker for permission to use some of their fascinating information that has not yet been published.

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10

Dynamics of Nutrient Supply in Plantation Soils

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Abstract

Maintaining the nutrient supply in soil is crucial for sustaining productivity. Nutrient budgets, which compare the balance between input and output fluxes with the amount of nutrients in the soil, provide useful information for making decisions on the long-term supply of nutrients. The nutrient content of forest soils is very variable, both spatially and depthwise, and some forest practices (soil disturbance by mechanical harvesting, windrowing, slash burning) can increase that variability further. Data to construct nutrient budgets can be obtained by appropriate soil surveys and stratified sampling of soils. Measurements of input and output fluxes of nutrients can be used to make budgets describing the dynamics of nutrient supply in plantations. Budgets for one full rotation period can be obtained by including data on nutrient losses during harvesting and site preparation. Losses of nutrients during harvest and site preparation may far exceed the rate of their replenishment by weathering of minerals in soils or by input via precipitation, especially when rotations are short. For maintaining high growth rates in short-rotation plantations, inputs of nutrients as fertilizers, especially of P and cations, will often be required. Management of such plantations should reduce or minimise nutrient losses, for example by retaining bark and crown slash on the site at the time of harvesting, distributing slash uniformly on the site (avoiding heaping), minimising use of fire for slash removal, distributing ash on the site, reducing the erosion potential (especially that of ash materials), and using undergrowth to capture and retain nutrients at risk of leaching. Opportunities for managing site nutrition through the planting of mixtures of species, or alternating species in successive rotations, deserve consideration. The development of these strategies will require additional research, especially on mineralisation, silicate weathering, nutrient and water interactions and cation equilibria.

THE DYNAMICS of nutrient supply in forest ecosystems are primarily driven by transfer processes within the ecosystems and those associated with the input and output of elements. To understand the flows of elements in forests and their effects on productivity, one can use the concept of an ecosystem model. A forest ecosystem can be visualised as consisting of compartments which may include chemical elements in various vegetation components such as foliage, wood, bark and roots, in the litter and humus layers of the forest floor, in soil organic matter, in the soil solution and on the sorptive surfaces of the soil minerals. Various processes such as litterfall, nutrient uptake, mineralisation, immobilisation, cation exchange and anion retention link the different compartments (model elements) within the forest ecosystem. Inputs of chemical elements via precipitation (wet and dry deposition), fertilizer additions and mineral weathering, and outputs via harvesting, volatilisation (fire) and leaching connect the various segments of the model with the environment.

In an undisturbed natural forest, input and output of each element is expected to be equal. In these circumstances, the nutrient cycle is closed and the system is said to be in a steady state. However, the steady state does not exist in all phases of development in a natural forest and in a uniform way throughout a forest site and over the landscape. During the life cycle of the forest, gap formation and regrowth are recurring events; they can occur simultaneously on adjacent sites. When gaps are formed the balance of C and nutrients is negative because of loss of biomass, mineralisation and leaching of elements, whereas during the regrowth phase balance may be restored through the production and accumulation of biomass. As the steady state can be expected to occur only for short periods and nutrient inputs from the atmosphere are insufficient to compensate for losses from the system, the store of weatherable minerals is gradually consumed. This is one reason why many soils of the humid tropics are poor in nutrients.

Even-aged plantations differ from many natural forests in that the phases of gap formation (harvesting) and growth (stand development) form an easily-recognised sequence in time. When a plantation is growing, biomass production exceeds decomposition, while at harvest and during site preparation for establishment of the next crop the export of organic matter and nutrients, and the decomposition of organic matter, are dominant processes. Most plantations are established on cleared forest land, logged-over primary or secondary forest, or on poor agricultural land. Plantation operations may cause downgrading or upgrading of the soil properties, depending upon the practices used. Successive plantation crops can be expected to deplete soil nutrient reserves because of the export of nutrients with the harvest and potential losses via volatilisation, airborne ash, soil erosion and leaching, depending upon management.

Studies describing nutrient relationships in tropical plantations—especially those providing information on the amount of nutrients in soils and vegetation and which influences many management decisions—are limited. Examples of questions which would benefit from such information include how harvesting (wood and bark) and slash should be managed to reduce nutrient losses, or the measures required to compensate for nutrients lost. Such issues, pertinent to sustainability of forest production, are of more significance in the tropics than in temperate zones because in the tropics rates of production are high and the soils are usually poor in fertility. Despite this deficiency in the data base, available information does provide a basis for making sensible operational decisions.

In this chapter we identify some of the key factors that affect nutrient cycling processes in plantations. Firstly, to assess changes in soil properties and the significance of those changes for forest productivity, it is essential to describe the range and variability of nutrient pools in plantation soils, which we do below. Secondly, after discussing methodology for studying nutrient changes in soils, soil processes relating to nutrient balance (nutrient losses and gains) under plantations are described. Finally, nutrient transformation processes in soils are discussed, with special emphasis on N and P. The problem of generalisation for tropical plantations is considered from a wider perspective by extrapolating results of process-oriented studies from a given site to others where boundary conditions (site characteristics) and other factors affecting tree growth and soil fertility may change.

Variability of Nutrient Stores in Forest Soils

The fertility of soils in the tropics varies greatly (for discussions refer to Richter and Babbar 1991; Lal and Sanchez 1992; Chapter 4) when the following soil and fertility parameters are considered:

- soil organic matter (humus),
- N, P and S stores,
- exchangeable base cations (K, Ca and Mg), and
- the exchangeable acid cations (H, Al, Fe, Mn and NH_4) — soil acidity.

In this section, spatial variability in the above soil parameters will be considered at four scales: a) supra-regional; b) regional; c) plantation operational area; and d) compartmental (operational unit) level.

Variability in soil properties across regions

The amount of organic matter in a soil depends on the quantity of biomass at the site and the rate of organic matter turnover. In a humid tropical lowland soil under forest, soil organic carbon in the 0–100 cm horizon normally lies in the range of 75–125 t ha^{-1}. The amount increases with elevation, as low temperature slows the decomposition of biomass faster than its production. According to Zinke et al. (1984, in Jordan 1985), the increase can amount to about 40 t ha^{-1} per 1000 m, reflecting a corresponding change of 6°C in mean annual temperature.

Soil acidity also influences the amount of organic matter stored in the soil by retarding decomposition processes (Jordan 1985) by:

- reducing the microbial and faunal activity,
- producing scleromorphous leaves containing small amounts of proteineous substances (N, P and S) and large amounts of structural material. C:N (and also C:P) ratios of such materials are high—in the range of 20–30 instead of the usual range of 10–15, and
- forming relatively stable Al-organic matter complexes.

These factors result in the development of a layer of decomposing organic matter on the surface of the mineral soil which may amount to 50–120 t ha^{-1} of organic matter (25–75 t ha^{-1} C) (Table 10.1—soils C and D). In stands on richer lowland sites, forest floor biomass may range from a few tonnes to 50 t ha^{-1} (Table 10.1—soils A and B, refer also to the review by Binkley 1995) depending on the tree species. In the fast-growing species in the tropical environment the amount of organic matter accumulated on the forest floor within 7–8 yr may be less than 10 t ha^{-1} (Rhoades 1991 quoted by Binkley 1995). The amount of N accumulated on the forest floor will vary depending on whether the trees are N-fixers or not. For example, in stands 5.5 yr old in Puerto Rico, the amount of N (kg ha^{-1}) accumulated was 133–138 for *Leucaena leucocephala*, 156 for *Albizia procera* and 256 for *Casuarina equisetifolia*, all of which are N-fixers, compared with 100 for *Eucalyptus robusta*, which does not fix N (Wang et al. 1991). These values are relatively small compared with the total amount of N in the soil which, for example, varied from 2.2 t ha^{-1} to 7.1 t ha^{-1} for the 0–50 cm horizon in four soils representing a range of fertility (Table 10.1). Total P in the soils can range from <150 kg ha^{-1} to >1000 kg ha^{-1} (Tables 10.1 and 10.2) depending mainly upon their silicate content (the less weathered sandy soils and volcanic ash soil in Table 10.2 had the higher soil P values). In forest soils the fraction of the total N mineralised annually is usually less than 5% and in most cases less than 1%, and varies spatially and temporally depending upon the conditions of mineralisation (quality of soil organic matter—C:N ratio, amount of lignin and phenolic compounds; environmental conditions—temperature and moisture; and microbial activity). In addition to the factors mentioned above for N, however, plants play an important role (by producing enzymes and organic acids) for decomposition of organically-bound P.

The abundance of base cations and soil acidity are inversely related. They can be expressed as % base saturation or as mass of elements per ha and soil depth. The latter is preferable because the values for each element and/or horizon can then be summed. The amount of cations varies among soils, depending primarily upon annual rainfall and stage of weathering and soil formation. The magnitude of variability can be appreciated from the data given in Table 10.1 for four representative soils from contrasting environmental conditions. Soil A is derived from young alluvial deposits which are rich in silicate minerals and are in the early stages of weathering. It has a large amount of base cations. A young soil derived from volcanic ash material under similar climatic conditions may have even more base cations than shown under A in Table 10.1. Early stages of weathering and soil formation may also be found in regions with rapid erosion. The soils are then relatively shallow.

Table 10.1 Organic matter on the forest floor, and total C, N, P and exchangeable cations, and cation exchange capacity (CEC), to a depth of 50 cm for four humid tropical soils of widely differing fertility under natural forests. Soil A is derived from young alluvial deposits, West Llanos, Venezuela, annual rainfall 1650 mm; soil B is on metamorphic rock, SW Nigeria, annual rainfall 1350 mm; soil C is on an older terrace in Magdalena Valley, Colombia, annual rainfall 3000 mm; and soil D is on early Pleistocene sediments with low evergreen forest in the Middle Orinoco piedmont, Venezuela, annual rainfall 2400 mm

Attribute	Atypical (rich) A	Typical (less humid) B	Typical (more humid) C	Atypical (poor) D
Organic matter on the forest floor (t ha^{-1})	2	5–15	15–50	50–120
Total soil C (t ha^{-1})	58	63	81	47
Total soil N (t ha^{-1})	7.1	6.20	5.40	2.20
Total soil P (t ha^{-1})	1.4	0.82	0.73	0.55
Exchangeable soil cations				
K (kg ha^{-1})	460	650	119	67
Mg (kg ha^{-1})	960	290	43	16
Ca (kg ha^{-1})	7100	2580	31	7
Al (% of sum of exchangeable cations)	3	25	90	93
Ca+Mg/Al	90	4	0.11	0.06
CEC of soil (me $100g^{-1}$ clay)	60	10	5	2

Table 10.2 Total carbon, N and P, and exchangeable K, Ca and Mg in soils (0–30 cm) from different *Pinus radiata* plantations in the Sierra Occidental region of Chile. Site index is the mean height of the dominant trees at age 20 yr

Site group	C	N	P	K	Ca	Mg	Site index
	(t ha^{-1})			(kg ha^{-1})			(m)
Coastal dunes	12	1.2	1216	168	533	522	18.8
Sandy soils	37	2.4	1822	175	1029	135	24.5
Northern granite	56	3.8	351	370	3994	1267	23.4
Southern granite	98	5.6	336	772	2391	402	27.3
Northern metamorphics	62	4.0	354	366	1996	597	25.5
Southern metamorphics	95	4.9	255	211	1596	219	28.5
Northern red loams (basalt)	106	5.5	341	307	3590	864	26.9
Southern red loams (basalt)	114	5.9	141	472	2092	414	31.5
Volcanic ash	136	8.9	986	130	1726	138	28.9
Marine sediments	101	6.6	297	600	3036	951	30.8

Even under similar rainfall conditions the soils may show a wide range of base saturation, depending upon the type of rock and dominant clay minerals. The amount of bases may either be small due to kaolinite (soil B in Table 10.1) or large due to a high silicate content in young, less weathered and montmorillonite types of clay (soils from Kalimantan in Table 10.3). In weakly acid soils with high base saturation, Ca usually dominates the exchange complex. As Ca-containing silicates are weathered, however, the supply of Ca from this source to replenish losses is exhausted faster than that of Mg and K from more resistant minerals (mica, amphiboles). The saturation per cent of Ca on the exchange complex may then fall below that of K and Mg (soil C in Table 10.1), reaching such very low levels that it becomes a trace element (soil D in Table 10.1). Calcium plays a significant role in ecosystem functioning, because Ca functions in an ameliorative way against the toxicity of Al in cell physiology. Root vitality is strongly influenced by the Ca:Al ratio in the soil solution (Meiwes et al. 1984).

Soil acidification is a natural soil-forming process and given sufficient time, organic matter turnover and water percolation, all soils tend to increase their acidity. Rhoades and Binkley (1996) reported that pH of a soil (0–15 cm depth) declined under 8-yr-old plantations of *Eucalyptus saligna* from 5.9 to 5.0, and from 5.9 to 4.6 under *Albizia falcataria*. However, the decrease in base saturation is different at every soil depth. For example, the surface soil will always have a higher base saturation, so long as the forest ecosystem maintains a tight nutrient cycle, because cations are released in the surface soil during mineralisation of plant debris. Higher base saturation can also be expected at the depth where mineral weathering is occurring, a depth which will move downward with time. In younger soils, maximum soil acidity can be expected immediately below the surface soil. With increasing age of the soil, the acidification front will move downward following the weathering front, which is one of the reasons subsurface acidity is so prevalent in highly acid soils. This spatial variability in depth is important in relation to the potential development of the root system in depth. The abundance of base cations in surface soil can be changed by land use.

Variation in forest soil properties at a regional scale

Soils properties under *Pinus radiata* plantations in the coastal mountains of Chile will be used as a case study to describe variation in soil properties at a regional scale. The region stretches about 1100 km N-S, and from the coast of the Pacific ocean to 400 m a.s.l. Climatically it belongs to the subtropics, and climatic parameters include a N-S gradient in rainfall (annual rainfall 500 mm to >2000 mm). The variation in soil properties is related to variation in parent material and climate. The soils are relatively shallow, so that the amount of silicates, as well as their clay forming potential, is an important factor in the supply of base cations.

Gerding (1991) grouped Chilean plantation sites into 10 regional types (Table 10.2) based on the parent material, and reported large variation in the amount of nutrients and C. Parent rock had a distinct influence—e.g. granite soils were generally richer in base cations than those from metamorphic rocks; the basaltic to andesitic volcanic ash had a large Ca content from the weathering of Ca-feldspar glasses but was poor in K. The red loams were derived from basaltic rocks and were relatively rich in base cations. The importance of climate becomes apparent when soils of the northern and southern groups of metamorphic, granite and red loam are considered. The group of soils from the drier north had less carbon and more base cations than soils of the more humid south.

Table 10.3 Amount of K, Ca and Mg in the soil (kg ha^{-1} in 0–50 cm) and the expected harvest removal (kg ha^{-1}) by three species at age 20 yr in East Kalimantan. The top part of table provides values when stem wood only was exported, and the lower part when both stem wood and bark were removed. The mean annual growth increments were estimated to be 17, 15 and 36 m^3 ha^{-1} for *Eucalyptus deglupta, Acacia mangium* and *Albizia falcateria*

	K	Ca	Mg
Soil stores	320–780	615–3206	224–1275
Stem wood			
E. deglupta	231	172	32
A. mangium	174	102	24
A. falcateria	423	392	39
Stem wood plus bark			
E. deglupta	378	369	42
A. mangium	234	310	33
A. falcateria	478	460	46

Gerding (1991) analysed the influence of climatic and soil parameters on growth of *Pinus radiata* (Table 10.2) and concluded that all parameters relating to the water supply of the trees were of prime significance, whereas those relating to nutrient supply became important only within some groups (sandy soils, red loams).

Variation in soil properties within large regions like Chile may not be significant to a plantation manager operating at a local site. The manager will be concerned with soil variation resulting from variation of soil age (weathering depth) and relief, as well as any differences in parent material which may be present. Relief can be important because of down-slope movement of soil material and nutrients involving:

- transport of dissolved nutrients by lateral subsurface flow of soil water,
- erosion of ash by surface runoff,
- erosion of humus and nutrient-rich surface soil under forest, and
- erosion of soil during past geomorphic activity.

Variation in soil properties in an operational area of forest

An operational area for a plantation may form another level for studying variation in soil properties. For that purpose an area of 5000 ha of forest plantations in East Kalimantan, Indonesia, NW of Balikpapan was used as a case study. The area is hilly with moderate to steep slopes and the parent material of Tertiary silty sandstones to claystones. The soils are highly erodable and thus relatively shallow (1–2 m). Silicate content is low, but the clay fraction consists of 50% montmorillonite and 50% kaolinite. Cation exchange capacity is relatively high (22 milliequivalent 100 g^{-1} clay). Soils are typical Ultisols with Al-saturation of the exchange complex (below 20 cm depth) between 61% and 98%.

Ruhiyat (1989) and Brandes (1991) reported the following amounts of base cations in 0–50 cm soil depth: K 100–750 kg ha^{-1}, Mg 40–1600 kg ha^{-1} and Ca 60–3240 kg ha^{-1}. There was a close relationship between clay content and exchangeable K and Mg. In relatively young soils with a high CEC, the retention capacity of the soil for cations is high. A relationship between clay content and Ca was found only in soils from the upper slope and upper mid-slope; high Ca contents were observed in soils from mid- and lower slopes. The influence of slope position on Ca stores was greater than that of clay content. Ruhiyat (1989) also found that soils from mid- and lower slopes had more C (53–68 t ha^{-1}) compared with upper-slope soils (50–54 t ha^{-1}), indicating the importance of relief. On the other hand, slope position and aspect are expected to have less influence on the transient properties of a soil, for example, no effect of slope and aspect was observed on N mineralisation and nitrification rates (N cycling) in an upland pin oak forest in east central Minnesota (Zak et al. 1991).

Thus within a single operational area of plantation, great differences in soil nutrient reserves may occur, and these need to be taken into account in management practice. To assess these differences, slope position can easily be accounted for by using maps or air photos, while texture and depth require a ground survey. A greater investment would be needed to determine the residual silicate content of the geological strata. Good soil maps do provide a valuable basis for plantation management (see also Chapter 5).

Variation in soil properties at a compartment level

In a compartment, the basic territorial unit of a forest estate for purposes of record and management, the extent of variation in soil properties is expected to be smaller than for the landscape scales described above. This variation is examined by using experimental plots at Jari, Eastern Amazon. This site is located in the extensive forest plantation area north of the Amazon River in Eastern Amazon (Para) of Brazil. The soils were Oxisols derived from Late Pleistocene sediments, more or less strongly dissected to expose different sedimentary layers. Spangenberg (1994) studied soils from a number of experimental plots which varied in slope position, clay content and the number of previous rotations of fast-growing species. The soils were acid with low CEC values (kaolinitic material), and low in bases to several meters in depth. Stores of base cations (0–60 cm) did not show any relationship to clay content and slope position. The ranges of cation contents were: K 40–290 kg ha^{-1}, Mg 100–200 kg ha^{-1} and Ca 20–740 kg ha^{-1}.

These ranges in element concentration are narrower than those given above for the Kalimantan site because of the difference in scale of the two study areas and because the soils at Jari are much older and more deeply weathered. Differences in CEC due to variable clay content are small in these kaolinitic soils, and are easily obscured by the influence of geological strata. The history of the site, i.e. the number of rotations of fast-growing species, had a major effect on the Ca and Mg reserves of these soils (Spangenberg 1994).

Considerable heterogeneity in soil properties occurs at the scale of experimental plots. Scientists have long been confronted with the fact that physical and chemical soil properties vary on a scale of a metre or less, and this is specially so for soil parameters like net N mineralisation and net nitrification which are driven by litter inputs. The above examples show that the large soil variability that occurs at various levels in the overall ecosystem, and the way it may interact with management practices, need to be clearly recognised. Accordingly soil survey and appropriate sampling and planning to accommodate variation at a plot or compartment level are important considerations for both researchers and managers. Raison and Khanna (1995) suggested three key factors for increasing the efficiency and information content of soil samples: time scales sufficient to accommodate changes of specific soil properties, stratification of sites prior to sampling, and bulking by depth or horizon prior to analysis. At a plot scale, suitably stratified samples collected randomly (e.g. 24 replicates composited to 8 samples for analysis) allowed significant differences due to differing slash management (moderately burnt, ashbeds, unburnt) to be measured, but this information was lost when no stratification was done (Raison and Khanna 1995). It is important to recognise that the usefulness of soil-based information is limited by the extent of its variability at different levels of land use.

Methodologies for Studying Changes in Nutrient Content and Nutrient Cycling Processes

The development of a forest plantation, like any other form of land use, leads to changes in ecosystem characteristics and element fluxes. Most physical, chemical and biological properties of soils are also influenced. Reforestation of degraded land by appropriate management practices may result in a general improvement (upgrading) of soil fertility, while the establishment of a plantation after primary forest will, depending upon the intensity of site management, most likely initiate some degrading processes in the soil (decrease in organic matter content, decline in water-holding capacity, rapid mineralisation and loss of soil N), but also some upgrading ones (short-term release of inorganic P and cations, short-term accumulation of Ca released from the residual biomass). While a decision to convert primary forest into plantations can be either deplored or justified, a resultant change of site conditions has to be accepted once such a decision has been made. In most cases the conversion may mean a significant loss of biodiversity, forest biomass and nutrient content, and changes to the form and distribution of nutrients. The extent and speed of loss of carbon and nutrients can however be minimised if the processes are understood.

A number of methods may be used to measure change in the content and cycling of nutrients on a forest site due to either changed land use (from primary or secondary forest to plantation) or treatment (e.g. soil disturbance during harvesting and plantation establishment). Long-term observations extending from a few years to a full plantation rotation are required to assess the full impact of land use change or a management option in plantations. Some short-term empirical studies may also provide useful information. There are few studies in which changes in the nutrient cycling fluxes and processes have been followed over long periods. Examples of such studies are at Hubbard Brook, New Hampshire, USA and at Solling, Lower Saxony, Germany. There is a lack of long-term process-oriented studies of nutrient cycling in the tropics.

In the absence of long-term and regular observations, two other methods are widely employed. They are: a) retrospective studies and b) chrono-sequence studies.

Retrospective studies (for a discussion on this topic refer to Powers 1989) use the effects of treatments imposed in the past either deliberately (by design) or fortuitously (by accident, e.g. fire). Many studies reported in the literature which try to assess the effects on soil properties and productivity of planting a given species are examples of the retrospective technique (they compare ecosystem development in primary forest with that in plantations). A basic assumption of such studies is that the sites were initially comparable and the observed effects are primarily due to the treatment. Whether sites are comparable or not should be properly tested to avoid misinterpretation of the data.

Chronosequence studies consist of a time sequence of retrospective studies in which soil data from stands of different ages (treatments) are compared (for details of the technique see Cole and Van Miegroet 1989). The different stands represent stages in the sequential development of an ecosystem and its soil under a certain land use. It has also been described as 'false time' series because it assumes a similar initial ('time-zero') condition, and similar site conditions and events. Chronosequence studies may include process-based research. In most cases the original site conditions are not documented, and consequently uncertainties arise as to whether any difference subsequently evident between sites reflects an initial difference or is the outcome of more recent treatment (Hase and Fölster 1983; Bruijnzeel 1990).

Studies of both types can be pursued at one site, though the time over which the observations are made is usually restricted to a few years at best. Despite all the limitations, studies of both types have provided some useful information. Long-term effects cannot easily be followed using a true time series as the time required to arrive at statistically valid data is too long. So far as the soil is concerned, the reason lies in the high micro-scale variability (the high statistical error) of analytical soil data.

Nutrient Losses and Their Assessment

Nutrient removal by harvest compared with the amount in soils

Plantations are established for harvesting wood. Harvesting is one of the processes which diminish the nutrient content of the soil via biomass export. The extent of loss of soil nutrients is determined by a number of critical factors which include: management history of the site, tree species, rate of tree growth, nutrient content of biomass, rotation length, method of harvesting, nutrient reserves in the soil and other nutrient inputs (atmospheric sources). The potential need to replace lost nutrients to sustain productivity is sometimes ignored in forestry, probably due to the long rotations and the sometimes plentiful nutrient reserves in the soil, especially for slow-growing trees in temperate regions. As fast-growing, short-rotation plantations are being planted in the tropics on low fertility soils, however, the problem of sustaining soil fertility is an important management issue.

An example of the effect of management history of the site on soil nutrient reserves, compared with the export loss, is given in Table 10.4, taken from the study by Spangenberg (1994) at Jari and discussed previously. Nutrients exported at the harvest of stem and bark of *Eucalyptus urograndis* (a hybrid between *E. urophylla* and *E. grandis*) were compared for 3 treatments out of 13 studied.

The history of each treatment after clearing from primary forest was: Treatment a) represented a first-generation stand. Treatment b) had one rotation of 12 yr of *Pinus caribaea* and Treatment c) had three rotations of *Gmelina arborea* (altogether 14 yr). The losses of N and P were small when compared with the total amount of these elements in the soil. However the question is whether these small losses affect the mineralisation of N and mobilisation of P and thus their supply to plants in either the short or long term.

Table 10.4 Amount and nutrients in harvested stem wood and bark of 4.5-yr-old *Eucalyptus urograndis*, and left in 100 cm depth of soil, for three treatments at Jari, NW Amazon. Treatments are: a) a first-rotation stand; b) a second-rotation stand following first rotation of 12 yr of *Pinus caribaea*; and c) a fourth-rotation stand following three rotations (altogether 14 yr) of *Gmelina arborea*. Direct comparisons between treatments are hampered by lack of data on initial conditions and the possibility of differences between the soil reserves available to the different treatments

Treatment and material	Weight ($t\ ha^{-1}$)	Total N	Total P	Exchangeable K	Exchangeable Ca	Exchangeable Mg
					($kg\ ha^{-1}$)	
(a)						
Soil		12924	1350	150	1365	253
Wood	109	245	12	154	581	50
(b)						
Soil		3548	1268	45	435	117
Wood	91	204	9	128	452	42
(c)						
Soil		11686	3606	301	13	161
Wood	88	197	10	124	254	40

The amount of exchangeable Mg left in the soil always exceeded that exported with the harvest, but this was not so in case of exchangeable Ca and K (Table 10.4). The amount of exchangeable K and Ca remaining in the soil was well below the amount exported in several of the treatments. Most subsoils at Jari were nearly free of exchangeable Ca, a phenomenon which is rare even in tropical soils. The mean export losses of base cations for the 13 treatments during one rotation were: K 90 $kg\ ha^{-1}$, Ca 313 $kg\ ha^{-1}$ and Mg 32 $kg\ ha^{-1}$. Twelve of the stands were in the second to the fourth rotation, indicating that most of the previously grown *Gmelina*, *Pinus* or *Eucalyptus* had already extracted their share of base cations from the soil and left it greatly impoverished. Spangenberg showed (by a 'false time' series) that Ca and Mg stores in the soil decreased with the number of successive rotations.

The juxtaposition of exports and soil stores in Table 10.4 shows that the situation with respect of Ca and K is critical as very little of these elements is left in an exchangeable form in the soil. Additional losses by other processes (burning of residual biomass, leaching, erosion) cannot be compensated by any possible natural gain (e.g. by atmospheric deposition or mineral weathering), because of the restricted rooting depth in these plantations. There are also uncertainties regarding the minimum amount of nutrients which a stand requires to build up the optimum biomass on a site (Turner 1981). Spangenberg (1994) found no correlation between element concentrations in plants and element reserves in the soil except for Ca, indicating that plantations at the Jari site may have entered into a critical range of Ca supply.

The large content of Ca in 4.5-yr-old *Eucalyptus* (Table 10.4) was associated primarily with the high concentration of this element in the bark. Bark made up about 13% of the trunks, but it contained 87% of the Ca, 48% of the K and 68% of the Mg. Thus the practice of removing bark from a site requires serious consideration, including an economic assessment. Exporting bark requires additional inputs of 272 kg ha^{-1} Ca, 43 kg ha^{-1} K and 22 kg ha^{-1} Mg as fertilizer to compensate for the loss in each rotation.

Compensating for the nutrient export by fertilizer application (Fearnside and Rankin 1982; Jordan 1985; Chapter 11) poses both economic and technical questions. Most acid soils have high acidity in the subsoil. Movement of surface-applied $CaCO_3$ into the subsoil is very slow; even high rainfall in the humid tropics may have very little effect on Ca transport. For example, fertilising and liming of continuous cultivation trials at Yurimagua, Peru, after 7.5 yr reduced acidity only to 45 cm soil depth (Bandy and Sanchez 1986). The rate of transfer of surface-applied Ca to 50 or 100 cm depth remains unknown. Bark is used in Jari to generate energy: is it feasible to return ash to the field? Is ash a useful material (Ohno and Erich 1990) or will it behave like conventional liming material? Studies on the solubility of Ca in ash (Khanna et al. 1994) indicate that ash behaves in soil like other liming material.

In a separate study at Jari, Russell (1983) estimated losses of a similar magnitude for 11-yr-old *Pinus caribaea* and 8.5-yr-old *Gmelina arborea*. For a 6-yr-old *Eucalyptus* species with a biomass similar to that given by Spangenberg (93 t ha^{-1} wood and bark), Jorgensen and Wells (1986) estimated a potential export of 170 (N), 14 (P), 262 (K), 312 (Ca), and 52 (Mg) kg ha^{-1} of nutrients. Species differences were evident from the study by Ruhiyat (1989) of 5–10-yr-old plantations (Table 10.3) in East Kalimantan of *Eucalyptus deglupta*, *Acacia mangium* and *Albizzia falcateria* on different soils (data on the soils were discussed previously) and slope positions. Harvest was proposed at 20 yr of age and the yield was estimated by extrapolating existing growth curves which assumed annual increments of 17, 15 and 36 m^3 ha^{-1} for *E. deglupta*, *A. mangium* and *A. falcateria* respectively. The mean element concentrations for each species was used for the calculations.

Soils on upper slopes usually had small reserves of K and Ca. K levels in these soils may become critical, especially if *A. falcateria* is repeatedly grown. If the bark of *E. deglupta* and *A. mangium* was not exported, the loss of K and Ca could probably be reduced by between one half and two-thirds.

A number of studies have compared nutrient export from a site with the reserves in the soil: Lundgren 1978 (*Pinus patula* age 7–30 yr, *Cupressus lusitanica* age 30 yr); Chijike 1980 (*Gmelina arborea* age 6–15 yr); Hase 1981, Hase and Fölster 1983 (*Tectona grandis* age 4–9 yr); Bruijnzeel 1982 (*Agathis damara* age 35 yr); Frederick et al. 1985 (*Eucalyptus regnans* age 4–17 yr); Vibrans 1986 (*Pinus elliottii* age 20 yr); Gerding 1991 (*Pinus radiata* age 15–33 yr); Birk 1993 (*Pinus radiata* age 20–21 yr); and Waterloo 1994 (*Pinus caribaea* age 5 yr). When data from these studies were expressed as the ratio of a given nutrient exported: soil store, large differences between both sites and elements were recorded, the values ranging from 0.5 to >1 (Vibrans) to 0.02 (Lundgren). Such a ratio may be useful in characterising the status of nutrient supply in a given plantation site. Fassbender and Bornemisza (1987) proposed this ratio as an expression of long-term ecosystem stability (high ratio = unstable, low ratio = stable) with respect to nutrients.

The main problem of using such ratios lies in standardising the soil data: for example, the depth of soil used to estimate the soil stores varied among studies from 30 to 100 cm. As nutrients from deeper soil layers can be depleted during successive rotations, it would be useful to analyse soil down to a depth of 100 cm (refer also to Bruijnzeel 1990). There is also debate about the forms of soil nutrients which should be included as soil stores, for example Bruijnzeel (1982), Gerding (1991) and Waterloo (1994) have suggested that non-exchangeable base cations be included, whereas elements which might be dissolved from silicates would require consideration before they can be included (see later discussion under 'Nutrient Gains'). As to the nutrients in the above-ground vegetation, one could consider the amount present in the stem wood and bark as a first approximation, despite further nutrient losses which may occur during site transformation between rotations. An index based on the amount of nutrients in (stem wood + bark)/(their amount in 0–100 cm soil) may be described as a plantation stability index, PSI(total). Because of the relative importance of the bark, it is also useful to assess the ratio of nutrients in (stem wood only)/(soil store), and describe this as PSI (stem wood).

The length of rotation greatly influences the rate of export of nutrients through harvesting, as growth rate and nutrient concentrations in bark and stem wood of younger trees are generally higher than those of older trees (Gerding 1991; Turner 1981; Chapter 11). Jorgensen and Wells (1986) demonstrated this with data of Castro et al. (1980) of 8- and 18-yr-old stands of *Pinus oocarpa*: the younger stand with 60% of the stem and bark biomass of the older one contained 77% (N), 84%

(K), and 92% (P) of the respective element stock of the older stand. Crane and Raison (1980) compared P removed when harvesting *Eucalyptus delegatensis* and *Pinus radiata* forests on short and long rotations. From *P. radiata* stands of >7 yr, 3–5 times more P was removed for a unit weight of log harvested than for *E. delegatensis* of the same age, because sapwood in *P. radiata* persisted for 17–25 yr (cf. 7 yr for *E. delegatensis*) and the concentration of P was much greater in sapwood than in heartwood. Moreover, the concentration of P was 3–10 times greater in the heartwood of *P. radiata* than it was in *E. delegatensis*. Furthermore, short-rotation plantations are subjected to more frequent losses during the transformation phase (between rotations, see below). A more detailed account of these issues is given in Chapter 11.

Assessment of nutrients in the harvested biomass (stem wood + bark)

In order to estimate the amount of nutrients in the harvested wood and bark the following steps are recommended:

1. Measure total stem volume of the stand at the time of harvest or extrapolate it from the growth curve of the stand or of harvested plantations of the same species in the region.

2. Calculate stem volume under bark. This parameter can be derived either by assuming the bark to be a particular fraction of the total volume, or by measuring the thickness of the bark at a representative diameter (over bark) and deriving underbark stem volume as a function of bark thickness and diameter over bark.

3. Obtain nutrient concentrations (g m^{-3}) in the stemwood (without bark) for a given species (or a similar species) from literature; the element content per ha can then be obtained by multiplication of concentration with the volume. Note that the presence of heartwood may affect nutrient concentration in the stem.

4. Element concentrations in the bark are usually available in literature. The amount of each element with bark can be calculated from the weight of the bark, estimated from stemwood underbark volume.

Assessment of nutrient stores in soil

The amount of soil nutrients should be determined with due consideration of variation (see earlier discussion) caused by geological strata, slope position, etc. Wherever possible soil should be sampled to a depth of 100 cm. For comparisons of soil data, morphological soil horizons as sampling strata are not adequate because their thickness may vary: instead, fixed depth increments are preferable. For situations where soil changes due to management practices are expected to occur mostly in the surface soil, more differentiation near the surface is beneficial, for example, 0–5 cm (or even 0–2.5 cm), 5–10 cm, 10–20 cm, 20–30 cm, 30–50 cm and 50–100 cm.

In order to account for the high spatial variation in soil properties, a minimum of 12 points per site of 50 m × 50 m should be augered. For analysis, samples can be reduced to 3 by mixing. C, N and exchangeable base cations (use unbuffered salt if possible) can be analysed with standard methods with fairly comparable results. In order to convert concentration data (mg or m.e. 100 g^{-1}) into kg ha^{-1}, the apparent densities of the depth strata sampled need to be measured. Methods to assess soil acidity (H, Al, Fe), base saturation and soil P differ widely, and the results cannot always be compared. For measuring mobilised (plant-available) forms of N and P in soils, additional effort will be required as described near the end of this chapter.

Intensities of site disturbance and changes in soil nutrients

Nutrient supplies are most disturbed during conversion of land from native vegetation (primary forest) to plantation, or from one plantation rotation to the next. Operations during site preparation and plantation establishment, apart from harvesting, may include slash management, cultivation, planting and tending. Management scenarios resulting in increasing disturbance after clear-cutting are:

1. Harvest, removal of logs, mulching the slash and planting
2. Harvest, removal of logs, burning the slash and planting
3. Harvest, removal of logs, extraction of stumps and coarse roots, burning and planting
4. Harvest, removal of logs, extraction of stumps, removal of slash and stumps (windrowing) and planting.

After harvest, processes that affect the nutrient store and soil chemical properties are:

- Input of nutrients from aboveground slash (crown, undergrowth, litter) to the soil surface and from the root system below ground. The amount of nutrients contained in the above- and belowground residues depends upon the amount of slash and its nutrient concentrations (usually higher than those of stems) determined by the species and the age of the stand. The relative importance of the slash and its distribution will be considered below.
- Decomposition of slash, stumps and roots commences, releasing nutrients. The rate of decomposition is increased by warmer and moister microclimatic conditions. As relatively few roots remain alive, the uptake of water and nutrients by plants is minimal, resulting in an imbalance in nutrient release and uptake. An excess of water on the site may result in losses of nutrients via leaching (see below), depending on soil physical characteristics (Smethurst and Nambiar 1995).

- When the residual biomass is burnt, additional losses of nutrients occur by particulate transfer or volatilisation during the burn or by erosion (see below) following fire.
- The soil is compacted by mechanical operations, reducing the volume of soil which can store water (reducing water-holding capacity) or which can be exploited by tree roots for water and nutrients (reducing rooting volume). Mechanical operations will be considered below.
- Transformation of nutrients in the soil, influencing not only their form but also their retention characteristics (see below).

Management of logging residues for nutrients

Plantation slash consists of tree crowns, undergrowth, roots and the litter layer; all of which can contribute to the nutrient supply of succeeding crops. Published data on nutrients in slash refer mostly to tree crowns only, although sometimes undergrowth is included. We evaluated data on slash from 119 stands of 12 tree species given by 11 authors (Egunjobi and Bada 1979; Chijioke 1980; Bruijnzeel 1982; Hase and Fölster 1983; Nwoboshi 1983, 1984; George 1984; Pereira et al. 1984;, Ruhiyat 1989; Gerding 1991; Spangenberg 1994; Waterloo 1994). The amount of slash ranged from 10 to 90 t ha^{-1}. Factors such as species, tree age, productivity and stand density (management) also varied but the relative importance of each was not easy to quantify. The data by Bruijnzeel, Ruhiyat and Nwoboshi showed the influence of age (Table 10.5); for similar studies from nontropical areas the reader is referred to Madgwick et al. (1977), Frederick et al. (1985) and Gholz et al. (1985). Crowns form a high proportion of total biomass in young stands; their importance decreases as the stands age. Species differ in the proportion of biomass and in the nutrients accumulated by their crowns.

The amount of slash as a fraction of aboveground biomass was about 20% for *Pinus caribaea* (6–10 yr, Egunjobi and Bada 1979; 15 yr, Waterloo 1994), *Eucalyptus urograndis* (5 yr, Spangenberg 1994), *Eucalyptus saligna* and *E. citriodora* (9 yr, Pereira et al. 1984), and *Eucalyptus* hybrids (10 yr, George 1984), 11%–19% for *Tectona grandis* (6–9 yr, Hase and Fölster 1983), 15%–35% for *Gmelina arborea* (6–15 yr, Chijioke 1980) and 16%–39% for 70 stands of *Pinus radiata* (15–37 yr, Gerding 1991).

The nutrients in the tree crowns account for a much higher proportion of the total nutrients aboveground in the stand than do those in other components, although the fraction varies with species. Conifers, with their lower element concentrations in the stem, fall in the upper range among tree species. For example, Gerding (1991) recorded a range of 52%–87% in the 70 stands of 15–36-yr-old *P. radiata*, Waterloo (1994) a range of 52%–86% in *P. radiata* (16 yr), and Egunjobi and Bada (1979) a range of 38%–67% in *Pinus caribaea* (6–10 yr). For non-conifers the proportion of nutrients in the slash is about 15%–25%

(Table 10.5, Ruhiyat 1989), 18%–37% for *Gmelina arborea* (Chijike 1980), 24%–46% for young *Eucalyptus urograndis* at Jari (Spangenberg 1994), 27%–(61)% for *E. saligna* and *E. citriodora* (Minas Gerais, Brazil, Pereira et al. 1984), 18%–42% for *Eucalyptus* hybrids (India, George 1984) and 19%–43% (base cations 19%–30%) for 6–9-yr-old *Tectona grandis* (Hase and Fölster 1983). Even in short rotations of up to 10 yr this represents a nutrient reserve (kg ha^{-1}) of 250 N, 50 P, 280 K, 280 Ca and 75 Mg.

Table 10.5 Harvest slash (weight, and as a fraction of aboveground biomass), and the amount of elements (as fraction of the respective total in the aboveground stand), at different stand ages of *Agathis damara* (Bruijnzeel 1982), *Eucalyptus deglupta* and *Acacia mangium* (Ruhiyat 1989), and *Tectona grandis* (Nwoboshi 1984)

Species and age (yr)	**Slash**		**N**	**P**	**K**	**Ca**	**Mg**
	(t ha^{-1})	**(%)**			**(%)**		
Agathis damara							
35	36	18	36	48	36	41	49
19	42	19		47	29	52	59
11	22	29		33	68	63	48
7	20	34		76	77	72	82
Eucalyptus deglupta[a]							
9	10	12	80		48	34	53
9	10	10	73		46	32	56
7	9	12	80		59	38	63
5	9	21	77		60	44	61
Acacia mangium[a]							
7	12	12	48		57	31	58
6	14	21	55		64	39	55
5	11	19	58		64	39	73
Tectona grandis							
15		16	18	21	21	14	
11		27	19	31	21	16	
7		26	40	30	23	14	
1		56	60	66	54	46	

[a] Includes undergrowth

Expressed as the amount (kg) of nutrients per tonne of slash, the following approximate values were obtained for a range of species in 28 stands:

- N = <5 to 10 (<5 for *Gmelina arborea*)
- P = 0.5 to 1.5 (it is not clear whether site or species influence the value)
- K = 5 to 10
- Ca = 2.5 to 10 (some sites >10)
- Mg = <1 to 4

The relative importance of the litter layer is demonstrated by Lugo et al. (1990) who observed that the amount of litter in 10 plantations of different species ranged from 5 to 28 t ha^{-1} and the nutrients (kg ha^{-1}) from 55–187 N, 2–9 P, 15–46 K, 37–208 Ca and 17–43 Mg. The amount of nutrients was not related to litter biomass (more details are in Chapter 13).

Very little information is available on the underground biomass (see Chapter 8). Reis et al. (1987) studied above- and belowground nutrients of stands of *Eucalyptus grandis* up to 6 yr old on two sites in Brazil (Cerrado) and reported that roots contained 15%–30% N, 10%–25% P and K, 8%–28% Ca and 25%–35% Mg of the respective totals in the living biomass. Corresponding data by Bargali and Singh (1991) for 8-yr-old *Eucalyptus tereticornis* in India had much lower values (7% N and P, 18% K). Such variations are not necessarily genetically determined. Nutrient deficiency is known to increase the accumulation of root biomass.

Conversion of logged-over primary forest or older secondary forest to plantations results in even greater amounts of residual biomass on the site than is found when established plantations are harvested. In the former situations, non-commercial tree stems and the larger stumps form a much greater fraction of the total residual biomass, creating bigger operational problems. The stems may contain up to 75% of the base cations of the aboveground biomass and their values (kg ha^{-1}) may range from 160–300 for K, 262–311 for Ca and 70–152 for Mg (Fölster 1985). Stem wood and bark release nutrients slowly, matching the demand of the growing plantation trees, but their heterogeneous spatial distribution does not favour a uniform supply of nutrients to all trees. Even greater spatial heterogeneity in nutrients will be created on a site where the slash is pushed into windrows with or without subsequent burning (see earlier discussion).

In conclusion, harvest slash contains large quantities of nutrients, making it an important source of nutrients at the site. Their removal, for example by whole-tree harvesting, can have a serious adverse effect on soil fertility (see Chapter 11).

Burning of slash

Burning the slash is a cheap and simple way of clearing an area for planting. During the burn, however, nutrients are lost to the atmosphere by: a) volatilisation in element form; b) volatilisation in molecular form (organic compounds); and c) as ash particles. Nutrient losses as ash particulates depend upon the intensity of burn, the wind velocity (Woodmansee and Wallach 1981) and the moisture content of the residual biomass (Pivello and Coutinho 1992). Smith and Bowes (1974) estimated that particulate losses contributed about 30% of the total loss. Measurements of nutrient losses made by comparing pre-burn and post-burn debris do not differentiate between volatilisation and particulate losses. Raison et al. (1985a) assumed that Ca, because of its high temperature of vaporisation (1494°C) does not volatilise, as normal burns rarely exceed the 1000°C. Any loss of Ca would then occur as ash particles and the ratio of Ca to other elements can be used to estimate volatilisation. Mackensen (1994) applied this method with only partial success, as apparently the assumption of a homogeneous composition of the ash particulates may not always be realised.

Volatilisation of different nutrients in the element form follows their vaporisation temperatures in the order Ca <Mg <Na <K <S <P <N (see Raison et al. 1985a; Mortimer 1987). Mackensen et al. (1996) showed that P volatilises slower than S, and Mg faster than P, Na and K, and concluded that the type of bond and molecular volatilisation probably resulted in these variations. Relative ease of volatilisation according to him followed the sequence N>>S>Mg>K, P, (>)Na> Ca. For a more thorough treatment of the topic, see Raison et al. (1985a).

Data on volatilisation losses of nutrients (Raison et al. 1985a; Mackensen et al. 1996) are few and restricted to N and P; when available they are rarely accompanied by appropriate information on fire conditions. The values vary with the type of material burnt. An additional problem which further complicates comparison of results arises when the pre-burn residual biomass is weighed and analysed without any consideration of the timing of the sampling after cutting or before burning. This can lead to variable results, because of losses via leaching of elements from the dead material (Khanna and Raison 1986). Mackensen et al. (1996) measured the loss of elements from two field sites with 33 and 96 t ha^{-1} of residual biomass of a secondary forest in Eastern Pará, Brazil. Leaching losses from the residual biomass during drying, i.e. between cutting and burning, are compared with the total loss of nutrients from the slash during fire (Fig. 10.1). Na and K, to a lesser extent also P, are mobilised during this leaching phase. Leaching of K from dead leaves has been known, but that of P has not been reported except by Ewel et al. (1981). Leaching of cations from the dead biomass does not necessarily mean a loss to the system. Some of these cations may be captured by the exchange complex of the soil or the roots of regrowing ground flora.

Loss of N occurs mostly as volatilisation and can be predicted from the loss of biomass and its N content. Percent loss of N corresponds closely to the relative weight loss of the residual biomass (Grier 1975; Raison et al. 1985b). N losses of >90% were found by Grier (1975), Pivello et al. (1992) and Mackensen et al. (1996), and of 83% by Ewel et al. (1981). In low-intensity burns, weight loss and N loss are correspondingly lower (Mackensen 1994). For the weight loss of >60% in a slash fire, Mackensen et al. (1996) calculated a loss of 50%–70% for S, 10%–30% for Ca and 20%–40% for Mg, but found no agreement with losses reported for K, Na and P.

For assessing the significance of the volatilisation losses, data from a number of sites are provided in Table 10.6. Site 3 represented a 6-yr-old bush fallow in Eastern Amazonia where the total biomass was burnt. The slash biomass on site 2

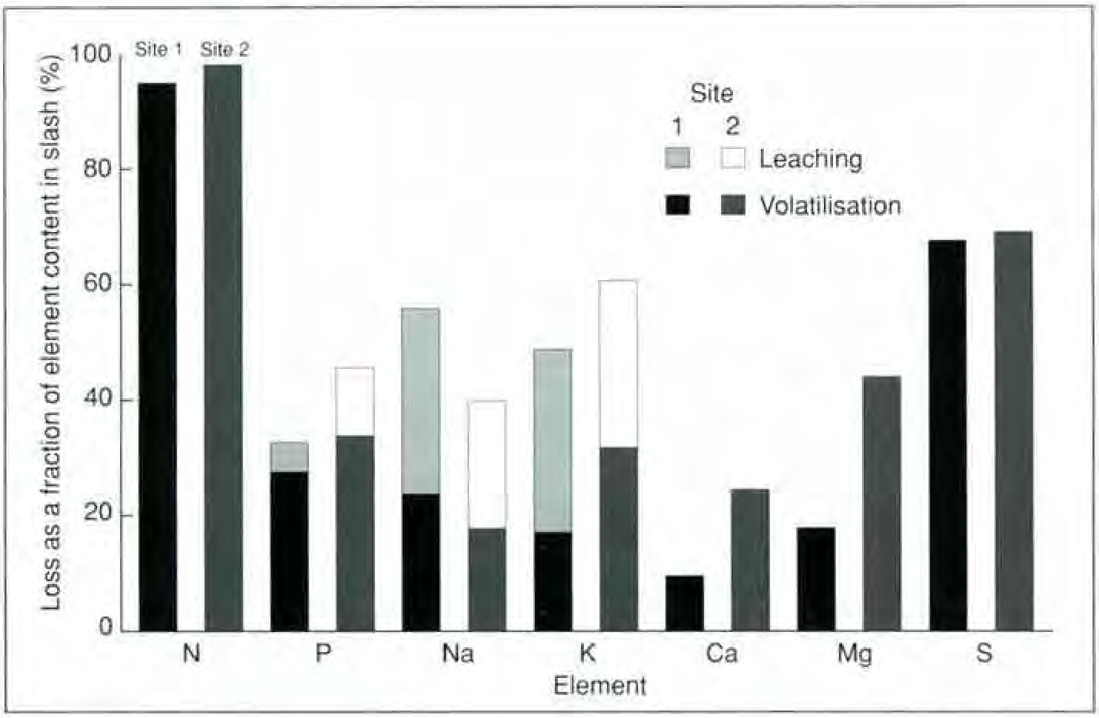

Figure 10.1 Nutrient losses on burning of harvest slash (left histograms 33 t ha^{-1} and right 90 t ha^{-1}) of a secondary forest in Brazil. The lower part of the bars indicates losses during the fire through volatilisation, and the upper part of the bars represents losses due to leaching from the slash before burning. All values are given as % of the element content of slash (Mackensen et al. 1996)

was probably at the upper end of the scale that could be expected in plantations (e.g. cf. Table 10.5), but equalled the amount of slash estimated by Ruhiyat (1989) after clear cutting a logged rain forest. The amount of slash at sites 1 and 3 fell within the expected range, although 50%–100% higher than measured by Spangenberg (1994) in a 4.5-yr-old *Eucalyptus* stand.

The fate of ash deposited on the soil surface at the end of the dry season depends greatly on the intensity and nature of first showers of the forthcoming rainy season; observations in the field (East Kalimantan) have revealed considerable surface wash of ash, especially on steeper slopes. Wind erosion can reduce the amount of remaining ash even before the rains start; the relatively great Ca loss on site 3, Table 10.6, was related to wind erosion.

Summarising, we conclude that it is hard to derive a generally acceptable procedure for assessing volatilisation losses of most elements, except N, despite recent progress in understanding the processes and the relevant factors involved. This is due to the complexity of interactions between fire intensity, composition of residues and volatilisation losses. However, the following general conclusions can be drawn:

- Higher-intensity burns consume greater amounts of residual biomass, usually of higher wood:leaf ratio, resulting in greater volatilisation losses and ash production. Low-intensity burns leave larger amounts of woody components in the field for slow mineralisation. If burning is unavoidable, low-intensity burning should be practiced.
- It is likely that a major part of the nutrients released during a slash burn will be lost either by volatilisation or by leaching of the ash, with Ca being an exception. Sim and Nykvist (1991) showed (Sabah, Malaysia) that *Acacia mangium* in 3.7 yr accumulated twice as much aboveground biomass when the slash of the clear-felled forest (logs extracted manually) remained unburnt than when it was burned (after tractor extraction of logs) (see also Farrell et al. 1981). Flinn et al. (1979) reported that burning of *Pinus radiata* logging residues in southwestern Victoria (Australia) would severely deplete nitrogen reserves and contribute to lower production in subsequent rotations. Emphasis in this case was laid on the strong depletion of N by both harvesting and burning of slash (28% of the total N 0–50 cm soil depth), and also of P.

Table 10.6 Nutrients lost by volatilisation during fire from different sites: at 1 and 2 slash was burnt after clearcutting of secondary forest in Brazil; the amount of slash on the two sites was quite different (Mackensen et al. 1996; see Fig. 10.1); at 3 the slash was that of a secondary forest developed during the fallow period of a small-farmers' rotational system in Brazil (Mackensen et al. 1996); at 4 different eucalypt forests in the Australian Captial Territory were burnt by prescribed fires (Raison et al. 1985b)

Sites	**Slash (t ha^{-1})**	**N**	**P**	**Na**	**K (kg ha^{-1})**	**Ca**	**Mg**	**S**
1.	33	325	2	3	12	28	6	26
2.	96	817	12	21	200	209	43	75
3.	31	199	4	6	35	102	17	34
4.	9–13[a]	74–109	2–3		12–21	20–30	4–10	

[a] litter + understorey

Leaching of nutrients

Addition of slash to the forest floor results in increased microbial mineralisation of organically-bound nutrients, causing a sudden increase in cation and anion concentrations in the soil solution. Depending upon the soil and environmental conditions (e.g. high rainfall in the early rainy season after the dry season) some of these mineralised elements may be leached beyond the main rooting zone in the soil, especially when there is a reduction in or even absence of living roots. It is important to recognise that enhanced mineralisation and leaching may occur even without burning of slash. For example, Uhl and Jordan (1984) reported a rapid release of nutrients after cutting primary forest on an Oxisol site in southern

Venezuela even before the slash had dried and been burned. Malmer (1993) observed a similar effect.

Data on leaching losses of nutrients during the conversion of natural forest to plantation and during the inter-rotation period of plantations are rare. Watershed studies have proven useful, provided the tightness of the watersheds could be ascertained, because such studies integrate local variability within the basin by measuring total water outflow from a large area directly (see Chapter 5). Inconsistencies relating nutrient concentrations in the outflow water may arise if the chemical composition of the leachate changes after passing through the rooting zone. For example if water passes through an alluvial substrate along the flanks of the stream channel, its composition may change due to cation exchange, dissolution reactions or plant uptake.

Soil water leaving the rooting zone can be sampled by lysimeters with or without tension, but these techniques do not provide reliable information on the amount of drainage. Therefore the water balance equation has to be solved (Chapter 5). There is still uncertainty concerning the likely variation in element concentration of water percolating through macropores (after heavy rains) as compared to ordinary matrix flow. For that reason, Radulovich and Sollins (1991) suggested that leaching of nitrogen and phosphorus in a well-aggregated, free-draining soil (Oxic Dystropept) from the humid tropics (Costa Rica) was best estimated by solutions collected from a zero-tension lysimeter. For obtaining reliable data on element flux, a combination of methods is preferred.

Bruijnzeel (1990) reviewed some studies in warm-temperate regions of south-eastern USA and eastern Australia (Fischer 1981; Riekerk 1983; Hewlett et al. 1984; Van Lear et al. 1985; Hopmans et al. 1987) involving clear-cutting natural or secondary forest (without fire), prescribed low intensity fires, or clear-cutting and burning of eucalypt forest, and concluded that nutrient exports through hydrological processes were either negligible or unimportant relative to those due to harvesting or burning (volatilisation). He ascribed these results to the small amount of drainage in the environments of the studies and postulated that in the tropics the losses of water and leaching of salts may be higher and occur at a faster rate. However, Hölscher (1995) in eastern Amazonia (1800 mm rain) studied nutrient drainage (by a lysimeter technique) within a 9-yr shifting cultivation system and also found that harvest and volatilisation contributed substantially more to nutrient depletion in the soil than did leaching (4%–27%).

Malmer (1993) studied nutrient export by leaching during conversion of logged primary forest to plantations. One catchment, named W5, was treated normally with tractor extraction of logs and burning the slash, while in another catchment, W4, operations were carried out manually and the slash was retained without burning. By comparing W4 and W5, with equal amounts of slash, the impact of burning was obvious, especially in the case of K. However, the nutrient loss by leaching was modest compared with the amount removed with the extracted logs (3–10 times for N, Ca and Mg: Sim and Nykvist 1991), or the amount that can be expected to have been lost during the burn, or compared with the amount contained in slash. Only about 10% (Mg 25%) of slash nutrients appear to have been leached in catchment W5.

We may tentatively conclude that losses of nutrients by leaching are less important than previously assumed and are less than losses due to harvest and slash burning.

Impacts of mechanised operations on nutrient cycling

Mechanised operations during harvesting, root and stump extraction, windrowing, redistribution of woody debris (for burning), and redistribution of ash, affect physical and chemical soil conditions. An important consequence is soil compaction which, apart from accelerating runoff and erosion (see Chapter 4) may also affect the extent of root penetration and the volume of soil exploitable by roots for water and nutrient uptake (Gent et al. 1983; Heinonen 1986; Chauvel et al. 1991; Cheatle 1991).

In Manaus, Brazil, Dias and Northcliff (1985) measured a loss of A1 horizon to an average depth of 5.7 cm in a windrowing operation. Based on the data from the undisturbed soil, it was estimated that there was a loss of about 22.5 t ha^{-1} of soil organic matter and about 20 (Ca, K) and 10 (Mg) kg ha^{-1} of exchangeable base cations. In a Nigerian soil (Ghuman and Lal 1991) with higher base saturation, the 0–10 cm soil layer below the burned windrows (one yr after forest clearance) had gained from the movement of soil and plant material from the cleared areas to the windrow about 7 t ha^{-1} of organic matter and of other elements (kg ha^{-1}): 390 N, 29 P (Bray-1 method), 228 K, 3900 Ca and 187 Mg. Morris et al. (1983) studied the effect of windrowing after harvest of a *Pinus elliottii—Pinus palustris* forest in Florida, USA. As the slash had been burnt before the operation, the windrows consisted mainly of woody components and soil. About 154 t ha^{-1} of soil were deposited in the windrows, an amount which the authors considered moderate compared with quoted examples of 300 and even 600 t ha^{-1}. These windrows contained an average of (kg ha^{-1}) 373 N, 18 P, 27 K, 163 Ca and 41 Mg which the inter-windrow areas had lost. These amounts represented 12% N, 33% K, 41% Ca and 20% Mg of the total soil store of the undisturbed ecosystem and were greater than the export loss in the harvest. In Liberia, Zech (1983) reported that mechanised clearing of rain forest with removal of organic matter and ploughing was detrimental to the nutrition of subsequently planted *Pinus oocarpa*, *P. caribaea*, *Gmelina* and teak.

Morris et al. (1983) pointed out that few trees in a plantation would profit from the gradual release of nutrients from the windrow material, as the windrows covered only 6% of the plantation area. Most of the mineralised elements will be leached at a rate depending on rainfall. They argued in favour of leaving the slash and the surface soil at its original place (see also Lal et al. 1986). Ghuman and Lal (1991) recorded a drop of Ca levels by 50%, and of K and Mg by 25%, in the fourth yr after clearing the forest. In nutrient-poor soils this amount of nutrient loss would lead to a decline in productivity of trees between windrows and this cannot be offset by additional growth of those growing on the windrows. Moreover, the irregular distribution of nutrient stores will result in irregular stands, further complicating growth inventories, other field records and systematic silvicultural treatment.

Nutrient Gains

Mineral weathering

Wittich (1942) was the first to emphasise the importance of non-exchangeable sources of base cations for the growth of pine plantations on north German sandy soils. His experiments suggested that even a small amount of silicate weathering could retard soil acidification and maintain a supply of base cations. In the cold temperate zone, rotations for timber production last 100–150 yr, and release of base cations from silicates can become important in such time spans. Increased acid inputs to forest ecosystems of the temperate industrial regions (acid rain), however, cannot be buffered to any substantial amount by the slow dissolution of silicates. In regions with a much lower input of atmospheric acidity, buffering by dissolution of silicates, at least in soils with a substantial reserve of silicates (or carbonates), may play a significant role—for example, in the humid tropics in shallow soils on certain rock types, in volcanic ash or younger alluvial sediments. The base cation content of primary silicates is usually not measured. Gerding (1991) found for soils under plantations in Chile that the ratio (total: exchangeable) for 8 soil types averaged 1.65 for Ca, 2.9 for K and 9.1 for Mg. Ca had a low value as Ca-containing silicates have a low resistance to weathering. As discussed previously, these soils are relatively rich in bases. These ratios are expected to be very close to 1 in typical Oxisols.

Information on the rate of release of elements by silicate weathering is controversial. There are four methods of data collection: laboratory experiments, long term balances of silicate depletion in soil profiles, and budgeting of inputs and outputs of watersheds and of soils by lysimeter techniques. The first technique has proved unsatisfactory because the length of water contact and the diffusion rates do not conform with those found in natural conditions, and the second suffers because the substrate homogeneity cannot be reliably determined. With the third technique, the researchers are confronted with the problem of proving the stability of the system i.e., no change in above- and belowground vegetation and that chemical processes below the rooting zone do not significantly change the composition of the solution entering the surface waters which are analysed. The problem with the soil lysimeters is that the soil solution collected by suction may not always be identical with the water percolating the soil, especially during macropore flow. A critical assessment of the last three methods is given by Bruijnzeel (1991).

Bruijnzeel (1991) reviewed input-output balances of 25 subtropical and tropical forest ecosystems, and related variation in the annual element loss (mainly base cations) to annual runoff, lithology and the state of weathering (and acidification). In Ultisols and Oxisols, losses ranged (kg ha^{-1}) from 5–15 Ca, 3–10 Mg and 9–21 K. These losses have been equated with weathering rates of minerals of the rooting zone and below the rooting zone. However the uncertainty in the methods and the implied assumption of a steady state warrants due caution when these data are used.

In summary, our present knowledge about possible inputs of base cations from weathering for uptake by plantations is limited by lack of suitable methods and site-to-site variation. However, it appears to be too small (Table 10.7) to compensate for nutrient export from plantations grown on short rotations. In plantations with longer rotations (20–80 yr), however, bases released through weathering may be an important input in some soils.

Table 10.7 Estimated quantities (kg ha^{-1}) of base cations released annually by silicate weathering in soils under forest plantations

Dominant vegetation	Silicate material	K	Ca	Mg	Reference
Agathis loranthifolia	Volcanic ash	11.6	18.1	25.4	Bruijnzeel 1982
Pinus caribaea	Basalt	< 5.7	< 6.1	< 9.9	Waterloo 1994
Tectona grandis	Volcanic ash	< 6.7	< 1.4	< 1.7	Hase and Fölster 1983

Atmospheric deposition

Nutrients from the atmosphere enter forest ecosystems in dissolved form with rain (wet deposition) or as particulates (dry deposition: aerosols, dust). Nitrogen is also added via atmospheric N_2 fixation, the amount of which is very small compared to N losses in plantations of non-N-fixing trees (they generally lack in N-fixers). Interplanting of N-fixing trees may present a useful alternative. For details on N fixation refer to Binkley and Giardina (this volume).

Nutrients analysed in water collected in rain gauges represent the wet deposition plus an unknown amount of particulate deposition washed out of the atmosphere by the rain. Additional nutrients in particulates captured by the forest canopy will be collected in the throughfall, but some may be absorbed by the canopy. Thus usual data available in literature on element deposition may underestimate total atmospheric deposition in forest stands. The amount of nutrients deposited may be affected by a number of environmental factors such as proximity to oceans, vulcanism and areas of regular burning (for a review refer to Bruijnzeel 1990), but the estimated ranges (kg ha^{-1} yr^{-1}) of element inputs are: 2–10 N, 2–8 K, 2-12 Ca and 1–5 Mg.

Within these ranges, lower values may be recorded at stations away from sources of inputs. As with weathering, we may assume that atmospheric deposition does not play any significant role in nutrient inputs within an individual short rotation, but it could be important for longer rotations or over several rotations. Figure 10.2 demonstrates the importance of the length of the rotation. Data included are: export data by Ruhiyat (1989); other losses (leaching, volatilisation and erosion) estimated by the same author using a 'false-time' series; and estimated means of deposition data. Differences between the two systems (short and long rotations) are partly due to greater total biomass and higher element concentrations in short-rotation harvests, and partly to the fact that element losses occur only once in the 21-yr rotation during site conversion, but three times in the same period under the short-rotation system.

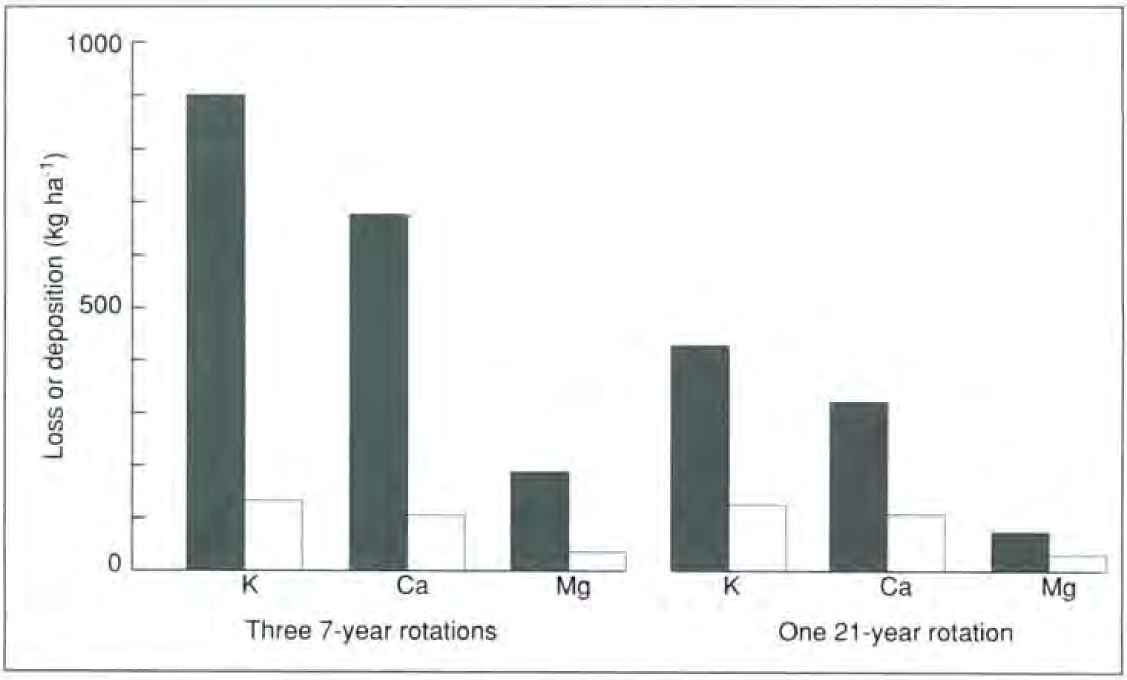

Figure 10.2 Total losses of base cations by harvest export, burning and leaching (left bars) and deposition inputs (right bars) during 21 yr of *Eucalyptus deglupta* forest plantation in East Kalimantan: three 7-yr rotations (left) are compared with a single rotation of 21 yr (right) (based on data from Ruhiyat)

Nutrient Transformations in Soils

Nutrients in soil exist in different forms, both organically and inorganically bound, but their uptake from the soil solution by roots occurs primarily in mineral form following either mass flow or diffusion processes. Therefore the supply of nutrients to roots for uptake in most forest soils depends upon the amount of nutrients in the solution phase and (without major nutrient inputs from external sources) the rate of nutrient replenishment of and losses from the solution phase. Organically-bound nutrients (most N, some P, S, B and cations) are mineralised or immobilised primarily via microbial processes, whereas the inorganically-bound nutrients undergo cation exchange, dissolution and fixation processes, redox and complexation reactions. Among all the nutrients N and P are the two most important elements determining productivity in most tropical plantations, although base cations may become important in highly acid soils under repeated short rotations of fast-growing species (as discussed previously). In some soils, elements other than N and P may require special attention, for example, in sandy, mostly coastal, areas the supply of K and in highly leached soils that of B may be limiting. Zech and Kaupenjohann (1990) reported K and P deficiency in *Eucalyptus camaldulensis, E. torreliana* and *Casuarina equisetifolia* growing on sandy soils in southern Benin, Africa. Boron deficiency has been noted in many tropical countries, most recently in China (Dell and Malajczuk 1994). The capacity of soil to supply most of these elements depends upon the history of site preparation together with the inherent capacity of the soil to supply nutrients.

Changes in soil N

Most soil N occurs in an organically-bound form which should be mineralised to ammonium or nitrate before uptake by plants. Only a small fraction of the total N (less than 10% in most cases) may be mineralised during a rotation of a plantation. Mineralisation depends upon the quality of the organic matter (C:N ratio; lignin and phenolic content), environmental conditions and microbial factors. Other soil properties like pH (discussed previously), texture and mineralogy are also important factors because of their role in stabilising soil organic matter. In a study (Motavalli et al. 1995) on nitrogen mineralisation in a number of humid tropical forest soils from Costa Rica, Colombia, Peru and Brazil mineralogy of soils turned out to be a major factor, with allophanic soils showing higher mineralisation than soils with smectite, oxidic and kaolinitc mineralogies. Mineralisation is discussed in detail in Chapter 13.

In most soils mineralisation is a rate-limiting step in the supply of N to plants due either to the small amount of N mineralised relative to the quantity required for growth or to the lack of synchronisation in the demand and supply of N. The amount of N mineralised and the demand for N by trees varies during the life of a stand (Miller 1995). During the initial two to three yr of a plantation rotation, the amount of mineralised N is usually large (and it is especially so if the harvested slash is retained on the site) and the plant needs are small, which may result in some losses of N from the rooting zone either by leaching or through denitrification (Smethurst and Nambiar 1995). Thus application of N fertilizer during the initial period of plantation establishment may be of little value (Nambiar and Cellier 1985). Woods et al. (1992) have suggested judicious management of weeds to reduce such losses and to use weeds as a regulatory factor in the supply of N to trees. As the trees become older their demand for N increases and N mineralisation becomes a limiting step, i.e. all the mineralised N is utilised by the system. Depending upon the desired rates of growth under optimum soil moisture conditions, there may be a need to supply additional N as fertilizer at this stage (Nambiar 1990/91). In order to accelerate plantation growth, the application of fertilizer N at the time of thinning has also been recommended (Carlyle 1995). Application of fertilizer is an additional cost to the plantation manager. It also carries an environmental risk, especially in regions where the growth is highly seasonal and is coupled with seasonality in rainfall so that the need to supply N occurs when conditions are most conducive to its loss. Thus alternative methods of supplying N to plantations in the tropics, for example by developing mixed species plantings of eucalypt and acacia, are being considered (see Chapter 9).

The amount of N lost during slash burns associated with harvesting and in forest fires may vary from site to site (as described earlier), but on N-poor soils this loss may constitute a significant part of the total N and, in all cases, a significant part of mineralisable stores in the soil. Fire will also affect mineralisation processes by changing the micro-environment (soil pH, soil moisture and temperature) and microbial populations. In the short term, mineralisation processes may be accelerated (Bauhus et al. 1993; Serrasolsas and Khanna 1995) but in the longer term and following repeated fires, N mineralisation is likely to decrease significantly (Raison et al. 1992).

Uptake of NH_4 by plant roots (as of other cations) is by diffusion processes, whereas that of NO_3 is usually by mass flow which thus follows the transpiration stream. Of all the nutrient elements taken up by roots, the amount of N is usually the greatest (Khanna and Ulrich 1991), so that the form of N (NH_4 or NO_3) is a major factor in balancing charges for electrical neutrality in both soil and plant systems. Mineralisation is associated with the consumption and production of protons in the soil and, depending upon the fate of mineralised N (uptake, immobilisation, leaching to greater soil depths or denitrification), the net effect on the soil pH in most cases is to increase acidity (Khanna et. al. 1992) (the topic is further discussed in Chapter 14). These considerations have a number of implications for plantation management, such as the importance of developing practices to avoid excessive N mineralisation by judicious slash management, selection of species to plant, tillage and site preparation for planting, weed control measures and fertilizer application (timing, amount and form).

Any assessment of the N supply available from forest soils centres around measuring mineralisation of organic N. This poses special problems because mineralisation depends upon the active soil N pool (ASN) and the biological activity of the soil, both of which are affected by the highly dynamic soil environment. Most laboratory-based methods (potentially mineralisable N, hot KCl extractable mineral N, alkaline oxidation of soil N, soluble N in autoclaved soils and many other methods) are limited to assessing the ASN in soils. They are useful in describing any changes which might have occurred in soil N due to management practices. As an example, potentially mineralisable N predicted differences in the N supply of soils to a *Pinus radiata* stand 3 yr after receiving the treatments: control, continuous irrigation, and 400 kg of N ha^{-1} fertilizer application plus continuous irrigation (Khanna 1994), but not after 10 yr.

Of the methods available to measure N mineralisation under field conditions ('in situ'), the sequential coring technique of Raison et al. (1987) is widely used (Anderson and Ingram 1993; Knoepp and Swank 1995). Binkley and Hart (1989) reviewed methods of assessing N availability in forest soils. A number of plant methods are also used as indices of N supply. N concentration in fully grown young leaves has been traditionally used to assess severe deficiencies, but it has proved less useful to assess the N needs (fertilisation) or to determine changes in soil supply due to management practices: the high mobility of N in the canopy makes it difficult to interpret and use results of analysis. The N content of fine roots has shown some promising results; the concentrations of N in the litterfall (senesced leaves) of *Pinus radiata* has also been useful (Khanna 1994).

Changes in soil P

Phosphorus occurs in different forms in the soil, mostly as inorganic P of varying solubility, and as organic P. Organic P can form 10%–>90% of total P in forest soils, with >50% being a common value for surface soil. Mineralisation of organic P occurs through enzymatic reactions which are both microbially and plant mediated processes, and is therefore influenced by factors similar to the ones affecting N and C mineralisation, and by the activity of plant roots through the production of phosphatase enzymes. The amount of soluble inorganic P in the soil and the P content of plant roots have been reported to affect organic P mineralisation (see review of P mineralisation by Tate 1984). Soil and plant processes determining the supply of soil P include: physicochemical processes acting on inorganic soil components; and processes in the rhizosphere of plants, with and without mycorrhizae, causing solubilisation of inorganic P (production of organic acids), mineralisation of organic P (production of phosphatase enzymes) and uptake of P by mycorrhizal filaments. The tree species can significantly influence the biogeochemical cycling of phosphorus; for example Zou et al. (1995) found that soils of both *Alnus rubra* (and *Albizia falcataria*) had larger pools of labile P (both inorganic and organic) and greater acid phosphatase activity than soils of the conifers in Oregon (and *Eucalyptus saligna* in Hawaii). In addition to plants and microorganisms, microarthropods play a significant role in the cycling of P (Zou 1993). Recent studies by Illmer et al. (1995) suggest that sparingly-soluble inorganic phosphates may also be made available by proton excretion in the course of NH_4 assimilation by P-solubilising microorganisms. Such factors make the assessment of soil P supply in forest soils difficult.

Change in total P is not a good measure to describe management-induced changes in the P-supplying capacity of soil. For example, harvesting of logs would remove only a small fraction of total P from the soil (Turner and Lambert 1986), but probably a significant part of the mobilisable fraction of soil P. There are still problems of defining and measuring the mobilisable fraction of total P, but for all practical purposes one can regard it as the amount that becomes available (mobilisable P) during a plantation rotation. The amount of P removed by clear-cutting different eucalypt and pine stands 40 yr of age would be 7–79 kg P ha^{-1} (Turner 1981); expressed per tonne of wood removed this would range from 41 g to 313 g. The concentration of P in the wood and thus the quantity removed during harvest depends upon the relative fractions of heartwood and sapwood—for example *Eucalyptus delegatensis* trees 25-yr-old had outer sapwood of width 5 yr with P concentrations of 167–200 mg kg^{-1}, inner sapwood of 2 yr with 34 mg P kg^{-1} and heartwood of 18 yr with <15 mg P kg^{-1} (Crane and Raison 1980). Sapwood in *Pinus radiata* persisted for 17–25 yr so that short rotations of 7 yr of either species would remove a similar amount of P from the site (Crane and Raison 1980).

The method of managing harvest slash has a significant effect on the amount of inorganic P made available to the following crop. For example, retention of slash on a *P. radiata* clear-cut increased $NaHCO_3$—extractable inorganic P in the soil by 7.5 kg P ha^{-1}, which was adequate to sustain high early growth rates in the following crop (Bekunda et al. 1990). Burning of logging residues causes loss of P as particulates (ash transfer) in the smoke and as non-particulates (gas), the amount depending on the intensity of fire and the type of fuel. Factors affecting particulate losses have already been discussed above. Losses of non-particulate forms of P depend upon the composition of vegetation components (C:P ratio, cation content), and higher losses are likely in woody components (high in C:P ratio and low in cation content) (Raison et al. 1985a). Despite the loss of P due to fire, many authors have reported large increases of labile P pools in surface soil immediately after burning (Ellis and Graley 1983; Romanya et al. 1994). Khanna et al. (1994), however, reported that only a small fraction (<11%) of total P in the ash derived from combustion of *Eucalyptus* litter was solubilised by water. To assist the fraction of P in the ash to solubilise, the ash should be mixed with soil.

Burning may also affect the sorption and desorption characteristics of soils for P, depending upon fire intensity. Romanya et al. (1994) studied soil P fractions and P sorption/desorption characteristics 7 months after clearfelling and slash burning in a eucalypt forest. On a 10 ha harvesting coupe three microsites were differentiated: unburnt, burnt (medium intensity fire) and intensely burnt (ashbed sites). Phosphorus fractions were extracted from the soil with Bray 1, $NaHCO_3$, NaOH and H_2SO_4 methods. Adsorption isotherms were obtained by equilibrating soils with solutions having different concentrations of P and desorption of the ashbed P by extracting with Bray 1 extract. About 8 kg P ha^{-1} was deposited in ash. Labile inorganic P (Bray 1) increased from <1 mg kg^{-1} in unburnt soil to 5-13 mg kg^{-1} in the ashbed. Inorganic P in the surface soil layers increased markedly after fire. Ashbed soil also showed an increase in sorption capacity in the 0–5 cm soil layer, but the sorbed P was generally less tightly bound to the solid phase. As ashbed and burnt microsites represented 19% and 18% respectively of the surface area of the slash-burnt coupe in the native eucalypt forest, only a small fraction of the site was affected.

Application of fertilizer P may be essential for the success of plantations in many parts of the tropics because of the small amount of available soil P and high P-fixation capacity of Oxisols, Ultisols and Alfisols of the tropics. The amount of P required for optimum growth of trees will depend upon soil characteristics and expected growth rates of the species used (Chapter 11). Because of low efficiency of utilisation of fertilizer P, splitting fertilizer into a number of small applications is often desirable.

A number of chemical extraction procedures have been developed and used with varying success to assess mobilisable P fractions in forest soils (Ballard 1980). Other methods used in recent years are: chemical fractionation techniques (Bekunda 1987), sequential extraction of soils by the Bray II method (Stewart et al. 1990), anion exchange papers (Saggar et al. 1990) and iron-impregnated filter papers (Menon et al. 1988). The iron-impregnated filter paper technique warrants special attention because of the ease with which it can be used under field conditions. Among the plant-based methods, P concentration in the foliage can be used to describe deficiency, while the P content of fine roots also seems promising (Pennell et al. 1990; Khanna 1994).

Synthesis

The value of determining nutrient fluxes and formulating nutrient budgets for understanding the dynamics of nutrient supply in plantations has been emphasised in this chapter. Even simple budgets of input/output of nutrients can provide useful information about changes in the nutrient status of a site. Such budgets should be developed for a period of at least one rotation, encompassing both establishment and harvest. Nutrient budgets are also useful for promoting basic understanding and assessing the relative significance of different processes as a basis for nutrient-related management decisions. Nutrient budgets can be considered only as good approximations of 'real world' happenings because of inadequacies of methodology; assumptions and extrapolations from 'false-time' series are usually required to supplement field data (Bruijnzeel 1990). The use of nutrient budgets in practical plantation forestry requires further consideration of restrictions imposed by boundary conditions (in space), tree species and rotation lengths.

The amount of effort needed to construct nutrient budgets for plantations depends on the level and sophistication of the information required for nutrient management. Simplified budgets can be based on knowledge of nutrient stores in soils and of losses expected in harvested biomass and through other pathways, by assuming that some processes play a more dominant role than others. Variability in measuring nutrient stores in soils is high to very high, depending upon the spatial scale (area) involved. Some forest operations (soil disturbance by mechanical harvesting, windrowing, slash fire) increase soil variability, and special techniques involving soil surveys and stratified sampling of soils are required to obtain useful data. Because of the time scales involved in measuring changes in nutrient stores and fluxes, retrospective and chronosequence studies ('false-time' series) are frequently used, but caution is required in interpreting data from such studies unless the comparability of sites is established. Combining retrospective studies with process-oriented ones can provide very useful information.

A number of nutrient cycling principles are crucial for describing the dynamics of nutrients in forest ecosystems (Khanna 1992): a) mass balance and conservation (as may be reflected in a budget); b) source and sink relationships; c) coupling and uncoupling of fluxes; and d) maintenance of electrical neutrality. Uses of budgets are mentioned above. Information on the sinks and sources in plants and soil is useful when attempting to modify system components, e.g. inputs, to achieve desired plant growth. Understanding the temporal and spatial coupling and uncoupling of nutrient fluxes is essential to decrease losses and to increase efficiency of fertiliser use. The importance of maintaining electrical neutrality in the soil-plant system cannot be overstated because of its effects on soil properties (e.g. soil acidity). Failure to achieve this can lead in the long term to soil degradation, especially in tropical plantations.

Ulrich (1994) described the functioning and stability of forest ecosystems in terms of material balance in the time and space involved in the processes leading to productivity. At the hierarchical level of ecosystem functioning where nutrient cycling processes become important in determining productivity, biomass producers can be grouped together into two categories: primary producers (growing plants) and secondary producers (decomposers). Ecosystems where the rates of the two producer groups come closer to each other are considered more stable. A stable system operates in an elastic range of nutrient fluxes, for example, it has similar amounts of input and output fluxes expressed on an annual basis. At the next hierarchical level of stand development, a forest manager has many options (species selection, soil cultivation, weed management, fertilisation, pruning, thinning, harvesting and slash burning) to affect nutrient cycling processes and thus the balance between primary and secondary producers. As the elasticity of nutrient fluxes in forest ecosystems has an important role in determining ecosystem stability, determination of changes (amounts and duration) in fluxes is a prerequisite for assessing the degree of stability. For example, a small loss of nitrate occurring for a short period after harvesting may indicate a small shift in the balance between primary and secondary producers and may or may not play a significant role in the productivity of a site.

Losses of nutrients during harvest and site preparation may far exceed the rate of their replenishment by weathering of minerals in soils or by precipitation inputs. Nutrient losses are higher when nutrient-rich components of trees (e.g. bark, tree crowns) are removed from the site or slash is burnt and the ash is partially or completely lost. For sustained high productivity of short-rotation plantations, additional inputs of nutrients as fertilisers will usually be required. Managers of such plantations should take the following steps to optimise nutrient supply:

1. Assess nutrient export via harvest and adopt measures to compensate for this ultimately unavoidable loss, recognising that loss at harvest is influenced by tree species and age. The significance of these measures will be evident when a comparison is made between available nutrient stores in the soil and nutrient losses via harvest and when emphasis lies on sustainable production.

2. Minimise avoidable nutrient losses (minimise bark, slash and litter export, slash burning, windrowing). The economics of management practices should be calculated with due regard to the costs of nutrient inputs required to offset losses.

3. Economise the unavoidable fertilizer inputs by matching them to demand in time (stages of growth) and space (widely spread or concentrated placement). A high rate of organic matter turnover at a site can contribute to a constant supply of nutrients. Experience of fertilizer application is available, but it is not automatically applicable to every site.

4. Include the dynamics of ground vegetation in management options not only from the perspective of competition but also as subsystem that aids nutrient cycling within the system.
5. Examine the possibility of using leguminous plants for N-fixation as an intercrop, or a leguminous tree species (which might be used as fuel) in mixture with other trees.

The identification of appropriate strategies and their efficient implementation will require additional research, in particular: i) to assess changes in the patterns of N and P mineralisation in plantations in response to management practices and plantation development, and to develop suitable models to predict mineralisation and its relationship to nutrient uptake by plants; ii) to assess the role of silicate weathering, cation exchange and cations in solution phases in determining cation equilibria and relate these equilibria to the quantity of cations accumulated in biomass during plantation development; and iii) to develop landscape-scale models which incorporate soil survey parameters to assess nutrient stores in soils, nutrient fluxes and tree productivity. Information from such research will complement that suggested by other authors elsewhere in this volume—for example on the understanding of nutrient and water interaction and its relationship to productivity—to assist plantation managers to consistently obtain good yields from their enterprise.

Acknowledgments

We wish to thank Dr J. Puhe for compiling a data bank which could not be included in the paper due to lack of space but formed the basis of a number of statements made.

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11

Soil and Stand Management for Short-rotation Plantations

J.L.M. Gonçalves, N.F. Barros, E.K.S. Nambiar and R.F. Novais

Abstract

Short-rotation plantations are a major source of raw material for wood-based industry, and particularly for the pulp and paper industry in the tropics. They are also widely used for poles, charcoal and fuelwood. These plantations are usually intensively managed to produce high yields. For their successful management a good understanding is required of the interaction between water and nutrients, and the influence of these factors on stand development. Depending on the level of productivity they may have high uptake demands on the nutrient reserves of the generally poor tropical soils. Fertilizer application has been a common practice to increase productivity. Its effectiveness, however, depends on soil water availability, the source and application strategy of fertilizer and other stand management practices. At each harvest, the amount of nutrients removed through harvest and the loss of nutrients through intensive site disturbance can be substantial. Appropriate site and stand management techniques are therefore required to conserve and recycle as much nutrient as possible at the site to maintain nutrient availability. Examples of practices in Brazil are discussed to illustrate principles and options in relation to sustainable management.

INTENSIVELY-MANAGED PLANTATIONS in tropical and subtropical regions have been established largely on land where temperature and rain are conducive to high plantation productivity. The climate and the productive capacity of soils in which plantations have been established vary enormously (see Chapters 3, 4 and 10). At a regional scale, differences in plantation productivity can be partly attributed to climatic, soil and geomorphological variation leading to differences in the supply of nutrients and water. Because nutrient requirements of a stand are closely related to growth rate, intensively managed fast-growing plantations place large demands on soil nutrient reserves and available water. Seasonal deficiencies in water and nutrients and nutritional deficiencies are common in many tropical and subtropical soils. This may result in low or declining forest productivity if the soil and the stand are not managed properly. Silvicultural techniques can be applied to soil and stand management to improve the availability of water and nutrients throughout the life of a stand (Nambiar et al. 1984; Nambiar 1990; Nambiar et al. 1990). Experience in fast-growing plantations in temperate regions shows that scientifically-based, intensive management practices can increase and sustain productivity (Boardman 1988; Nambiar 1990, 91; Beets et al. 1994; Nambiar 1996).

In this chapter research data and silvicultural experience on industrial short-rotation plantations with emphasis on eucalypts are discussed from a Brazilian perspective, with some additional examples from other relevant cases. The paper can be seen as a case study, but an important one, because it is based on a prominent example of industrial plantation development using exotic species designed for a particular end-product. The productivity and sustainability of these plantations remain a topic of much attention and speculation. Organised plantation forestry in Brazil began late in the 1960s, stimulated by a government policy which subsidised afforestation programs from 1967 to 1989 to develop an internationally-competitive wood-based pulp and paper industry, managed by the private sector and based on the experience and feasibility of growing and using eucalypt wood for pulp and paper production (Campinos 1991; Ondro et al. 1995). By 1995, Brazil had established six million hectares of forest plantations (5 million ha eucalypt and 1 million ha pine) over a wide geographic area and managed with a variety of silvicultural techniques to achieve a range of productivity. They are harvested in a 7–10-year cycle mostly for pulp but also for charcoal. From a biophysical viewpoint, these plantations have much in common with plantations in other tropical and subtropical countries and thus provide an appropriate base for discussion of prospects and problems of developing and maintaining plantations of introduced species.

In Brazil, most of the soils being planted to fast-growing species are Oxisols which are generally deep with variable texture. These soils have medium to good water storage capacity but are low in nutrients, especially phosphorus and cations, and occur in regions where dry seasons last for two or more months. Nutrient deficiencies and water stress are the main constraints to plantation growth; sound soil and stand management practices including nutrient additions are necessary to obtain yields that approach the maximum potential of the sites and to ensure the economic viability of the industry. Large areas of these plantations now have second-rotation crops with research and management addressing sustained productivity. The potential constraints on high and long-term productivity and management practices that can minimise or overcome those constraints are discussed below.

Water Availability

Rainfall is one of the most important climatic variables that influence forest productivity in the tropics (see Chapter 3), and its distribution is used as a criterion with which to classify tropical climates. The annual rainfall of tropical and subtropical areas ranges between a negligible amount and 10000 mm. As a general pattern, rainfall decreases as latitude increases, but elevation, land form and other site conditions may strongly affect this relationship. The length of the dry season may also increase with the latitude, beginning with practically no dry season in regions close to the Equator. Rainfall is greatest during the summer. On average, water stress limits plant growth for periods ranging from 8 to 12 months each year in 42% of tropical lands and from 4 to 6 months in 30% of the lands, while the remaining 28% is not subject to long dry periods (Sánchez 1976).

The soil-water regimes common in the tropics and subtropics are broadly classified into 4 categories (Soil Survey Staff 1975): i) **udic**—the soil moisture control section (SMCS) is not dry in any part for as long as 90 days cumulative during most years; ii) **ustic**—the SMCS is dry in some or all parts for 90 or more cumulative days in most year, but is moist in some part for more than 180 cumulative days, or it is continuously moist in some part for at least 90 consecutive days; iii) **aridic**—the SMCS is dry in all parts more than half of the time (cumulative); iv) **aquic**—a reduction region free of dissolved O_2 occurs due to saturation by ground water or capillary fringe. About 29%, 34%, 29% and 8% of tropical soils are classified in the udic, ustic, aridic and aquic regimes, respectively. These percentages are closely related to climatic types of the regions: 24% of rainy climates; 49% of seasonal, and 27% of dry and desert climates (Sánchez 1976). Fast-growing plantations offer their best potential in the udic and ustic soil water regimes, but good water conservation methods are most important to obtain economically satisfactory rates of production in all cases.

Soils used for plantations usually have a low to moderate water retention capacity. Ranzani (1971) classified the water-holding capacity of Brazilian savanna soils into four classes depending on textural composition: i) **very low**—sandy and sand-loamy soils, < 0.5 mm cm^{-1} of soil; ii) **low**—loam-sandy and loam-sand-clay soils, 0.6 to 1.0 mm cm^{-1} of soil; iii) **low to moderate**—loamy soils, 1.1 to 1.5 mm cm^{-1} of soil; and iv) **moderate**—clay-loamy and clay soils, 1.1 to 1.5 mm cm^{-1} of soil. For the same region, Lopes (1977) conducted an extensive survey of the physical and chemical characteristics of the soil and found that the largest amount of available water (water retained between 0.5 and 15 bars of tension) was obtained in soils with clay content ranging from 35% to 60%. Increases in the clay content above 60% did not result in increased water retention capacity in clayey Oxisols of the savanna areas that are strongly aggregated and behave as sandy soils, holding a relatively small amount of water. Forests planted under such conditions may experience water stress even during the rainy season because of rapid drainage.

Most of the short-rotation plantations presently located in Brazil are grown in regions where the mean annual precipitation varies from 800 to 1500 mm. In the Brazilian savanna, in soils with good physical characteristics, the availability of water can have an overriding influence on productivity. Figure 11.1 is a generalised description of the four climatic zones from the north-eastern (12°9' W longitude and 38°23' S latitude) towards the southern (24°15' W longitude and 49°43' S latitude) regions of Brazil, an area now extensively used for wood production for the pulp, plywood and charcoal industries. The productivity ranges for eucalypts and pines over 6–8 yr rotations are our estimates based on extensive experimental data. These estimates are good indicators of production under intensive silviculture. The main soils across these zones are low fertility, medium-textured Latosols. Despite the unavoidable confounding effects of site variation, there is a clear trend showing that as the water deficit increases the productivity decreases.

The strong interaction between soil types and rainfall on stem volume at a regional level was recently evaluated by Stape and Gomes (1996). Their study region was located in the north-east of the state of Bahia, Brazil (11°15' S to 12° 30' S latitude, 37°30' W to 38°45' W longitude, 0–300 m altitude). The mean annual temperature is about 25°C with small monthly variations, the highest and lowest means being 29°C and 20°C respectively. Plantations of hybrid eucalypt (*E. grandis* × *E. urophylla)* have been established on about 42000 ha over some years. The growth data (mean annual increment at age 5) from 1160 inventory plots collected between 1985 and 1995 are represented in Figure 11.2. Soil types were aggregated into 3 main groups with decreasing fertility: Ultisols, sandy loam - sandy clay loam (ult, sl/scl); Ultisol, sand-loaming sand (ult, s/ls) and Quartzipsamment (Qua). Mean annual rainfall ranged from <900 mm to >1500 mm. The three-dimensional representation of production clearly illustrates the strong interaction between soil types (representing a gradient of fertility) and rainfall producing a wide range of MAI, from 12 m^3 ha^{-1} yr^{-1} to 48 m^3 ha^{-1} yr^{-1}. The amount of available water clearly had to be taken into account in deciding on strategies for site management and nutrient application.

The potential gains in production from the application of appropriate technology in relation to the interaction referred to above are shown in Table 11.1. The data are based on the aggregation of results from many trials and our experience. In another study in the Cerado region it was found that at a wet site the absolute increase in the response to N fertilizer was 26.9 m^3 ha^{-1} (19% greater than the control) whereas at a drier site the absolute increase was 5.5 m^3 ha^{-1} (50% greater than the control) (Barros et al. 1990).

To partially overcome the constraints on growth due to water deficits, species and provenance selection is of paramount importance. The photograph on page 384 shows stands of a drought sensitive species— *Eucalyptus grandis* and a more tolerant species—*E. camaldulensis*, under a large water deficit which killed many trees of the first species. The importance of taking into account the drought tolerance of species and the critical constraint on production at a site (usually available water) is obvious. The choice of soil and nutrient management strategies

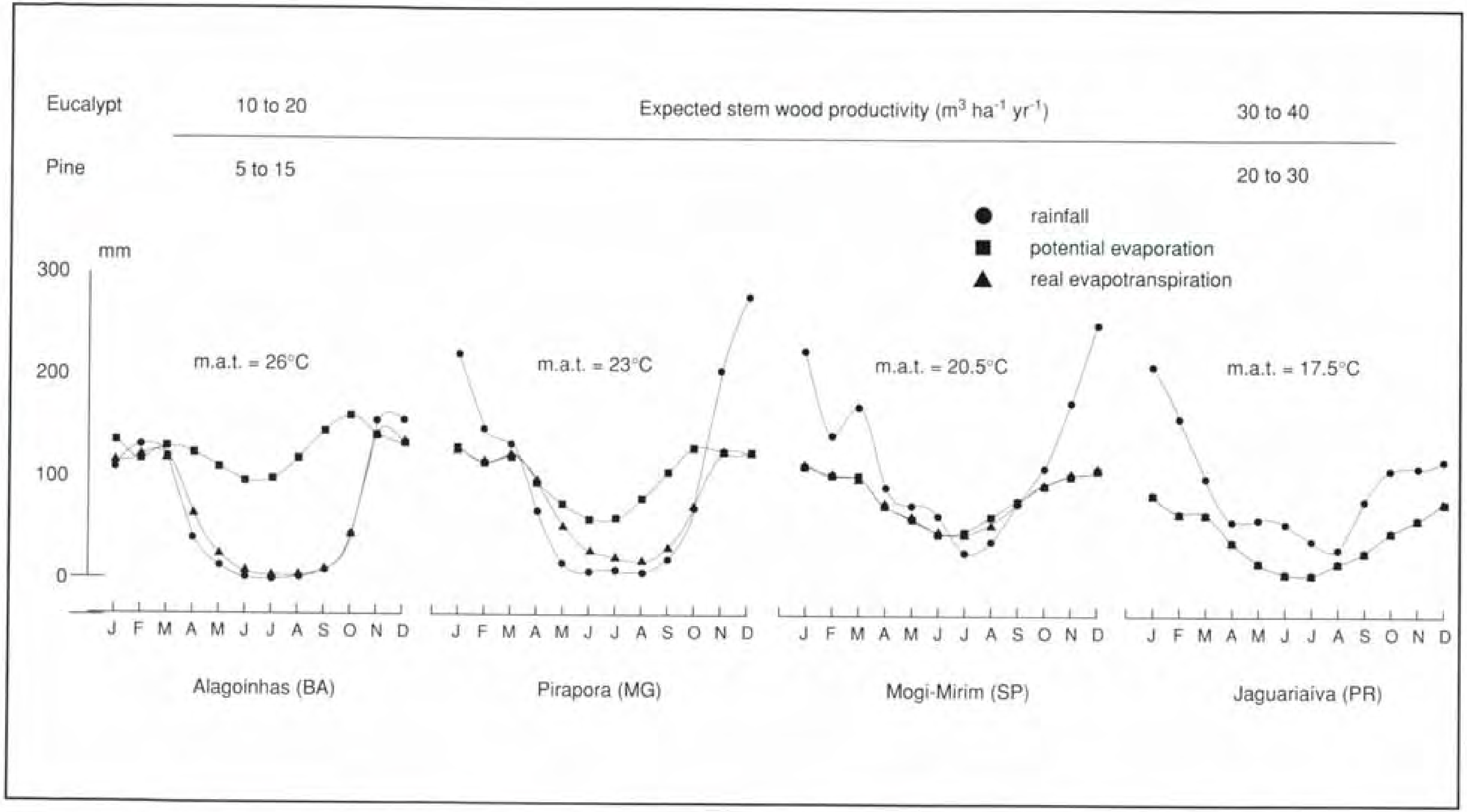

Figure 11.1 The range of rainfall, evapotranspiration and mean annual temperature (m.a.t.) from representative eucalypt and pine plantation regions in Brazil, with their productivity. The data apply to soils with poor fertility, medium texture and good physical characteristics

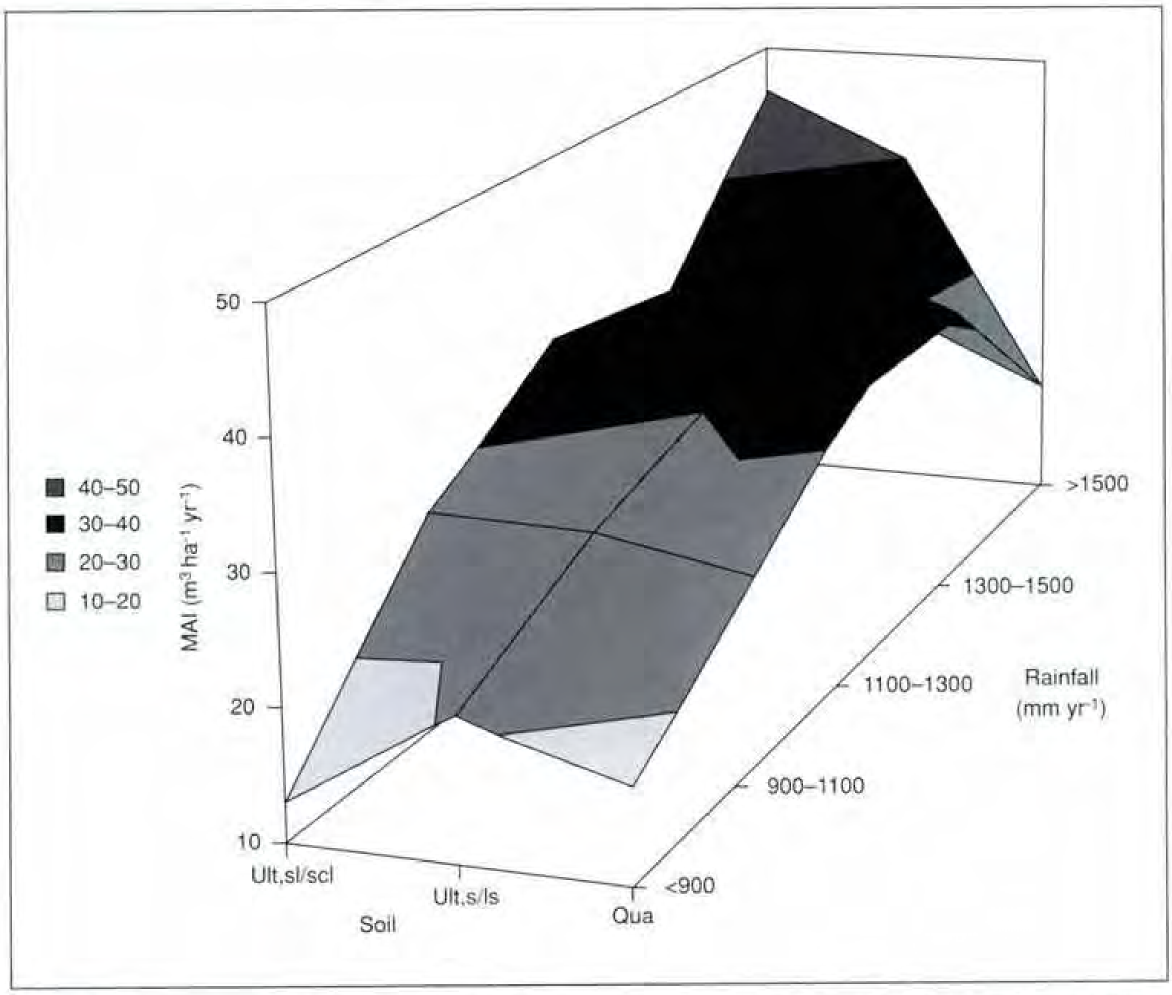

Figure 11.2 The interactive influence of soil type (representing a gradient in fertility and rainfall) on volume production of eucalypt plantation in the Bahia State of Brazil (see text for details) (Stape and Gomes 1996)

Stands of *Eucalyptus grandis* (at left) and *Eucalyptus camaldulensis* (at right), five yr old, suffering drought. (Photo: J.L.M. Gonçalves) (which entails estimating the likely return from fertilizer application), and the intensity of weed control required to minimise competition for soil water and nutrients, is dependent on understanding the effects of water × nutrient interaction on productivity (Fig. 11.2, Table 11.1, Fig. 11.5) in these environments (Nambiar et al. 1990).

Table 11.1 The net area planted to eucalypt plantations and plantation productivity in relation to the main soil types, rainfall distribution and the intensity of silviculture applied. The levels of silviculture (planting stock, site preparation, weed control and fertilisation) are referred as medium technology (MT) and high technology (HT)

Soil groups	**Number of months in which rainfall is expected to be greater than 100 mm**					
	9.5–12			**4.5–9.5**		
	Area (10^3 ha)	**MAI (m^3 ha^{-1} yr^{-1})**		**Area (10^3 ha)**	**MAI (m^3 ha^{-1} yr^{-1})**	
		MT	**HT**		**MT**	**HT**
Highly weathered and leached soils (Oxisols, Utisols and Alfisols)	920	25–35	35–55	1540	15–30	30–40
Sandy and shallow soils (Psamment and Lithic groups)	80	20–30	30–40	272	10–20	20–30

Nutrient Supply, Uptake and Tree Growth

Soil characteristics and nutrient supply

Most tropical soils are highly weathered, mainly because many of their parent materials are sedimentary and are subject to high temperatures and moist conditions. About 50% of the tropics are covered by Oxisols, Ultisols and Alfisols. A further 17% can be included in the Psamments and Inceptsol groups. These soil groups occur, predominantly, under rainy and seasonal climatic conditions (57% of the area) where the main forest plantations have been established (see Chapter 4). Some physical and chemical characteristics of representative soils used to establish forest plantations in Brazil are presented in Table 11.2. In these soils predominant clay minerals are kaolinite, iron and aluminium oxides, and amorphous materials containing only a small fraction of 2:1 type clay-minerals (Kitakawa and Möller 1977; Lopes 1977). Because of this mineralogical composition, the essential nutrient reserves are small, CEC is low, P-fixing capacity is high and soil aggregation is very marked, especially in the soils of the savanna region. The permeability of these soils and the potential to leach cations are high. The P, Ca, Mg, Zn, S, N, K, Cu and B levels in these soils are considered to be low or very low, and this has a major influence on the potential use and management of the soils. Successive short rotations of fast-growing species with a high nutrient demand would lead to marked depletion of the limited available nutrients and the small reserves in the soil. This could result in declining plantation productivity unless appropriate technical practices are adopted including nutrient input to the site.

Nutrient availability in the soil and uptake by trees, regardless of the soil fertility level, are strongly affected by the soil moisture regime. Within certain limits, the rate of nutrient uptake by plants is a function of nutrient concentration in the soil solution (intensity factor). This factor is controlled by soil characteristics that define the amount of nutrients retained in the soil solid phase (quantity factor) and the rate at which they come into equilibrium with the soil solution (capacity factor). The nutrient transfer processes between soil phases are influenced by characteristics such as ion exchange capacity, texture, soil compaction and particularly soil moisture. Several soil and forest management techniques can influence the availability of nutrients in the soil, and the choice of technique depends on the combination of site and soil conditions.

Table 11.2 Physical and chemical characteristics of soils representative of those used for eucalypt and pine plantations in tropical Brazil (adapted from Lopes 1977 and Vieira and Santos 1987)

Characteristic of top soil	Range
Clay (%)	6–50
pH in 0.01 M $CaCl_2$	3.8–5.5
Organic matter (g dm^{-3})	6–35
P-resin (mg dm^{-3})	1.0–3.0
Exchangeable K ($mmol_c$ dm^{-3})	0.2–1.2
Exchangeable Ca ($mmol_c$ dm^{-3})	0.4–5.0
Exchangeable Mg ($mmol_c$ dm^{-3})	0.2–2.5
Exchangeable Al ($mmol_c$ dm^{-3})	0.8–25.0

In tropical and subtropical regions, low P availability is one of the main soil factors limiting forest productivity (see Chapter 4). It has been suggested that about 65% of tropical soils are strongly P-deficient and 27% are moderately deficient (Roche et al. 1980). Additionally, many tropical soils have high P-fixing capacity because of their low pH and the predominance of ionic forms of Fe and Al and hydrous oxides of Fe and Al, which promote the fixation of existing or applied P in the soil and reduce the P available to the plants (see Chapter 10). Fertilizer application has been an effective way to increase P availability to the trees; complementary action on management of fertilizer can minimise soil P-fixation and increase fertilizer effectiveness (see later).

Thus the conservation of nutrients, nutrient additions and maintenance of soil properties to increase the availability of water are important pre-requisites for successful plantation forestry in Brazil. As noted in Table 11.1, the plantations in Brazil encompass a wide range in soils, productivity and responsiveness to silvicultural technology.

Effect of soil water regime on nutrient availability

The soil moisture regime is a factor controlling biological activity in the soil and, consequently, decomposition of soil organic matter (see Chapter 13). The dynamics of nutrients of the organic pool, both bound in the soil humus fraction and in the litter layer, are strongly influenced by soil moisture, because the temperature regime in the tropics in general (see Chapter 3) favours continuous microbial activity. Pilbeam et al. (1993) found that in an Orthic Ferralsol from Kenya, N mineralisation increased from 0.08 to 2.12 $\mu g\ g^{-1}\ day^{-1}$ as the soil water tension varied from 5.9 MPa to 0.06 MPa. In Australia, seasonal variation in in situ net N mineralisation has been reported in many studies and is often associated with changes in soil moisture or temperature (e.g. Raison et al. 1987; Smethurst and Nambiar 1990b; Gonçalves and Carlyle 1994). Despite the many factors that interact to determine net N mineralisation, Gonçalves and Carlyle (1994) were able to predict in situ rates on three of four occasions using only soil moisture and temperature variables in a simple model developed from an in vitro study.

It is a common field observation that the response of eucalypt stands to fertilizer applications in savanna areas in Brazil is much higher than that obtained in coastal areas (udic regime), despite the general similarity of the soil fertility of both areas. This difference in response has been attributed mainly to the better nutrient transport in the soil solution to the plant roots in the coastal area, where despite the low soil fertility larger amounts of nutrients reach the root surface. It is also common to observe symptoms of nutrient deficiency in plantations during the dry season, especially if dry conditions last more than 3 months (Barros et al. 1990 and 1992). One striking example is B deficiency which is now increasingly common in eucalypt plantations and aggravated by the occurrence of seasonal drought (Dell and Malajczuk 1994). Die-back and stem deformation of trees (see photograph on page 388) have been attributed to B deficiency (Gonzales et al. 1984; Dell and Malajczuk 1994); the intensity of symptoms increases with the duration of the dry season (Althoff et al. 1991) probably due to poor organic matter mineralisation and B transport in the soil. Deficiencies of other nutrients, such as S (Barros et al. 1990) and N, for which the soil organic pool is the main source, have frequently been observed in soils with the ustic moisture regime.

Dieback in *Eucalyptus camaldulensis* trees growing on a site with severe water deficit during the winter. (Photo: N.F. Barros)

To be absorbed by plant roots nutrients need to be released from the solid to the solution phase of the soil. The transfer processes between these two phases are mediated by mineral solubility, by oxidation–reduction potentials and by soil solution composition and ion concentration. All processes controlling the transfer and changes in form of nutrients are closely related to soil moisture content. When in soil solution, nutrients move towards the root surface by diffusion or by mass flow. Soil water content is one of the main factors affecting diffusion and ion activity in the soil solution. Olsen et al. (1965) reported a 10-fold reduction in the diffusion coefficient of various ions with a reduction of 10% in soil moisture content. Working with two tropical soils, Villani et al. (1990) found a reduction of 3.8 times in P diffusion in a clay soil when the water tension was changed from 0.01 MPa to 0.10 MPa. For a sandy soil a greater reduction (4.3 times) in P diffusion was observed for the same matric potentials. The effect of water–nutrient interactions on forest productivity is especially important for those ions such as P, Zn and Cu that are transported by diffusion and have an extremely small available pool of nutrients as is the case in the tropical and subtropical soils used for plantations.

The transport of ions by mass flow to the root system occurs in response to a gradient in water-potential created by the transpiration process. Therefore, for similar edaphic conditions, ion transport by mass flow and nutrient uptake by plants can be expected to be greater in regions with higher potential for transpiration. Likewise, under conditions of similar transpiration potential, nutrient uptake will be higher where ion fluxes and concentrations are higher, as they are related to soil moisture content and fertility level.

Root growth, and root distribution and configuration in the soil are other important factors influencing water and nutrient uptake and thus plantation growth. Dense root systems favour the uptake of poorly mobile nutrients that move by diffusion, because as a given volume of soil is more fully explored the distance for ion diffusion to the roots is shortened. Therefore, it may be expected that species which have abundant fine roots or can establish symbiotic associations with mycorrhizal fungi will have an advantage in the field, especially during the establishment phase, because they will be better competitors for water and nutrients (see Chapter 8). Studies on the development and configuration of the root system of trees in plantations can assist improvements in site management practices, especially those designed to increase water and nutrient uptake by young stands (Nambiar 1983,1990).

As mentioned before, high rates of forest growth are usually observed in regions where temperature and rainfall regimes favour canopy development and the capture of large amounts of radiant energy (see Chapter 6). Under such conditions, as the demand for nutrients is high, the ability of the soil to supply water and nutrients will determine forest productivity. As a consequence, a close relationship is found between biomass production and the amount of nutrients in the biomass (Fig. 11.3).

Nutrient uptake and tree growth

At any specific time in the growth cycle, several factors influence the quantity of nutrient taken up by trees, and consequently the probability of response to fertilizer application. These factors include total nutrient demand of the stand, growth rate, efficiency in taking up nutrients from the soil, and tree efficiency in using nutrients in growth processes.

Comprehensive studies on the fluxes of nutrients in plantations in the tropics in relation to the above topics are scarce. The available information refers mainly to the accumulation of nutrients in aboveground components of trees, and this may give a general trend of the amount and rate of nutrient uptake in such ecosystems. In Figure 11.3 we have plotted the mean rate of accumulation of N, P, K and Ca in the biomass in relation to the aboveground components of eucalypt plantations in Brazil, including several species, diverse site conditions and silvicultural management, and stand ages from 2 to 10 yr. The good linear fit of the equations indicates the close relationship between growth rates and nutrient accumulation in eucalypt plantations, similar to that reported for other tree species in general by Miller (1984). Given a productivity of 40 t ha^{-1} yr^{-1}, which does not include roots and litter, the mean annual uptake of N and Ca, the nutrients in greatest demand, is around 126 kg ha^{-1} and 109 kg ha^{-1}, respectively. Many soils in the tropics, with their low levels of organic matter and calcium (Table 11.2), may not be fertile

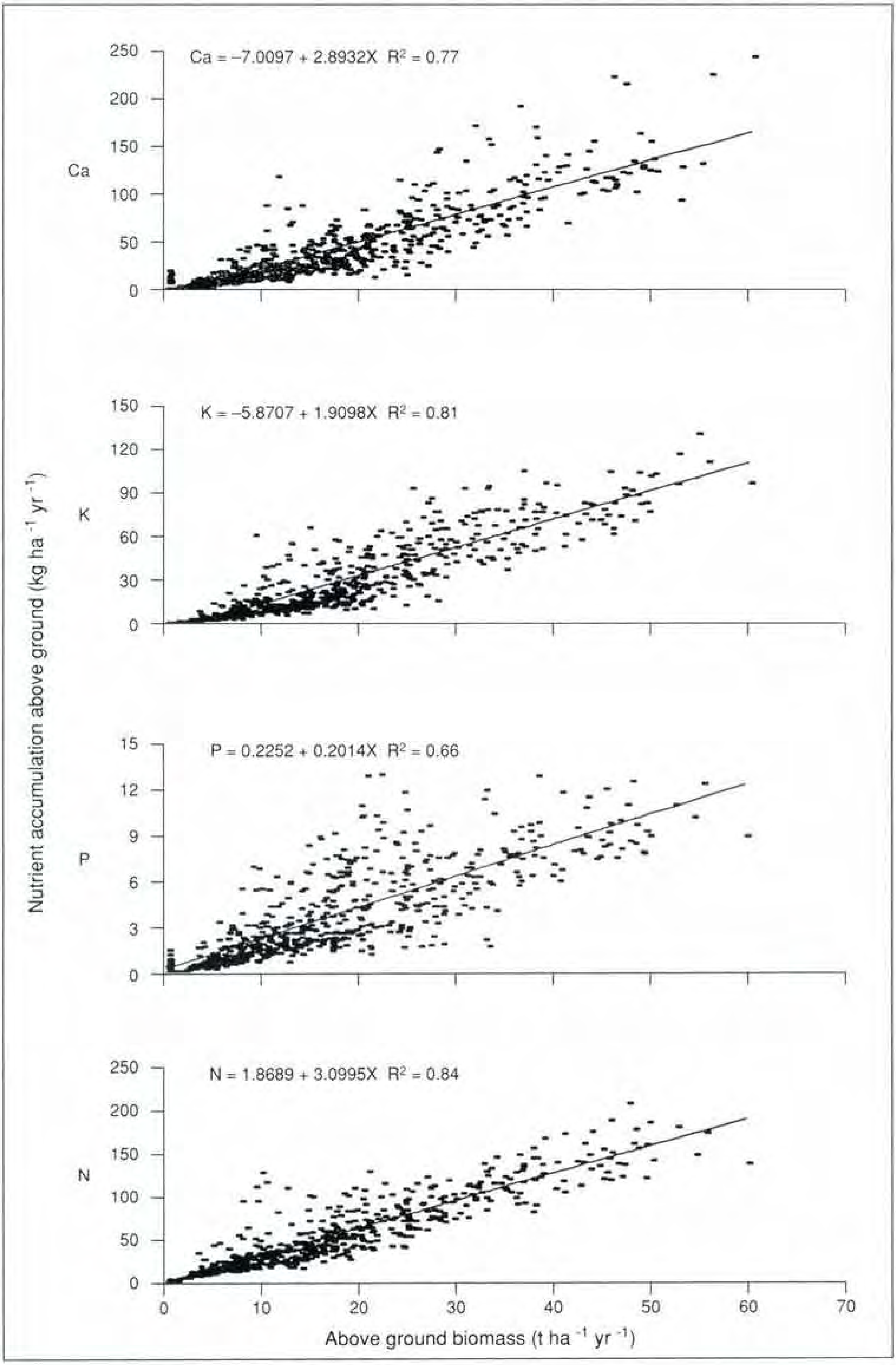

Figure 11.3 Rates of N, P, K and Ca accumulation in tree aboveground biomass of eucalypts in Brazil

enough to sustain high productivity, especially after the first or second rotation crops, without fertilizer application (Barros et al. 1992). The scatter of the points in the figures, particularly for P, may reflect, apart from factors such as sampling error, and differing fertilisation and rainfall regimes, variation in soil P-buffering power which has been shown to strongly affect P uptake by eucalypts (Neves et al. 1986).

The rate of nutrient uptake is not constant with stand age. Miller (1984) described three general nutritional stages in the life of a plantation. The patterns of aboveground biomass accumulation and nutrient accumulation in that biomass are described in Figure 11.4. During the first months after planting in the field the rates of nutrient accumulation are small. The length of this phase varies with site quality which is strongly influenced by soil water availability, especially in the subtropics and tropics. For example, in areas where rainfall distribution is uniform and soil water holding-capacity is adequate, the establishment period for eucalypts in Brazil is quite short — up to 1 month; in localities with well-defined drought periods, such as in the Brazilian savanna region, the establishment period may exceed 3 months. However, the time required for establishment in these cases is substantially shorter than is required even in warm temperate zones where this phase may take up to one year.

After establishment, the plants enter a stage of rapid growth and nutrient accumulation, especially if there is sufficient available water. The rate of nutrient absorption parallels the rate of biomass accumulation with age (Fig. 11.4). Only part of the soil volume is explored by the tree roots and the competition for water and nutrients between trees and other vegetation (weeds) can be very high in many circumstances (Lowery et al. 1993; Nambiar and Sands 1993). Bellote et al. (1980) and Reis et al. (1987) showed that most of the biomass and nutrient accumulated by *Eucalyptus grandis* planted in three sites in the Brazilian savanna occurred between two and five yr after planting, and this pattern is fundamentally related to availability of water (Fig. 11.4), once again showing the importance of water × nutrient interaction.

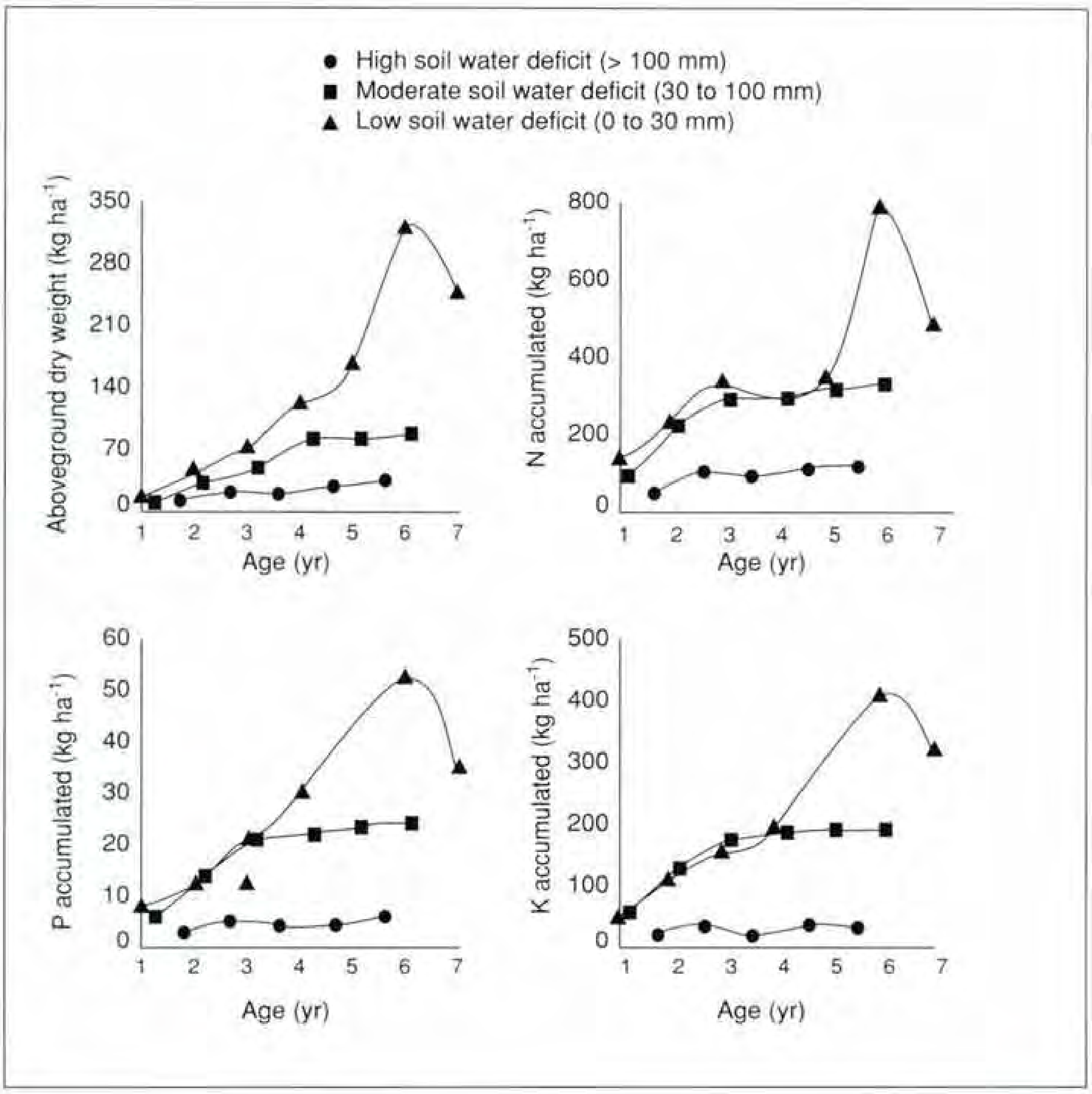

Figure 11.4 Changes in aboveground biomass, and nitrogen, phosphorus and potassium uptake with age of *Eucalyptus grandis* grown in three different sites of the Brazilian savanna region (adapted from Bellote et al. 1980 and Reis et al. 1987). In the savanna region the mean annual rainfall is around 1300 mm yr^1 and mean potential evapotranspiration about 1000 mm yr^1, both mostly (>80%) from October to April. The soil water deficit classes are based on the soil water balance assessed according to Thornthwaite and Mather (1955).

A stage with small fluctuations in the nutrient content of the living biomass follows canopy closure (Bellote et al. 1980; Castro et al. 1980; Reis et al. 1987). These fluctuations are usually due to seasonal variation in climate. Leaf shed may increase during long dry periods as a mechanism for reducing water loss, or in the beginning of the wet season when older senescent leaves are detached from the trees by wind (Reis and Barros 1990, see also Chapter 6). When the canopy is closed and leaf area stabilises, nutrient accumulation becomes relatively greater in the stem, and the litter biomass accumulated aboveground steadily increases to a level determined by site and stand factors (see Chapter 13). From this stage onwards a large proportion of the nutrient requirement of the tree is supplied by the biochemical and biogeochemical cycles (Miller 1995). Detailed knowledge of nutrient retranslocation (internal cycle) and the ways in which it is affected by nutrient supply in the soil and stand growth are not available for tropical plantations and this warrants research. In the savanna, the amount of N and P re-translated from senescent leaves of *E. grandis* (4– 6-yr-old trees) is about 75% of the amount contained in mature leaf (Reis and Barros 1990). The processes influencing the retranslocation of nutrients from young as well as senescing foliage in conifers have been described in detail by Nambiar and Fife (1991).

There are large differences among species in their ability to accumulate nutrients under different conditions of nutrient supply. Pereira et al. (1984) compared the biomass and nutrient allocations in 9-yr-old stands of *E. saligna* and *E. citriodora*, growing in an Oxisol of the Brazilian savanna region. They found that despite the very similar amounts of stem biomass (around 170 t ha^{-1}), in *E. saligna* about 50% of the Ca and 50% of the Mg accumulated in aboveground biomass was in the stem, whereas in *E. citriodora* the corresponding values were 72% of the Ca and 64% of the Mg. Furthermore, in *E. citriodora* 51% of the biomass K was in the stem compared to 64% for *E. saligna*. Similarly, Lugo et al. (1990 a,b) and Lugo (1992) reported large differences in the ratio between biomass accumulation and nutrient accumulation for N, P, K, Ca and Mg in several tropical tree plantations species under similar edaphic and climatic conditions in Costa Rica.

There are many reports in the literature of differences in 'nutrient-use efficiency' between species. In many cases this efficiency is estimated as the mass of dry matter divided by the mass of nutrient accumulated in the biomass. Such a ratio, based on a single measurement somewhere in the growth phase of a stand, is misleading in terms relevant to nutrient requirement or utilisation by trees. A more useful comparison is possible if the increments of biomass and nutrient accumulation are compared over several time intervals during stand development. Such a comparison is given in Table 11.3. In this study (Pereira 1990) measured the aboveground biomass production and nutrient accumulation of *E. grandis* and *E. urophylla* at 6-monthly intervals from planting to age 4 yr. Both species were growing side by side on an Oxisol in the Brazilian savanna. Despite the very similar aboveground biomass at age 4 yr, *E. urophylla* accumulated N and K at consistently higher rates than *E. grandis* during most of the incremental period. Expressed as efficiency, *E. grandis* produced 1.8 times more biomass per unit of N and 2.4 times more biomass per unit of K than *E. urophylla*. The amounts of litter and the nutrient concentration in them were similar among species. It should be noted that as the stand develops and the proportional allocation of biomass to different component change (cumulative increase of biomass in stem compared to foliage held at any one time), nutrient allocation would also change. Well-designed comparative studies on the pattern of nutrient accumulation and use from planting to final harvest of stand would be very useful.

Although tree improvement for high growth rates is, in general, paralleled by increased rates of nutrient uptake, there have been reports of differences in nutrient accumulation in components of different species (Montagnini and Sancho 1994), and in nutrient-use efficiency in tropical species (Wang et al. 1991). Miller (1995) suggested that differences between species have little to do with differences in nutrient demand between species, but rather reflect differences in their ability to obtain nutrients from intractable soil sources. However, in terms of managing soil resources, genotypic differences indicate avenues for refining nutrient management practices that are specific to sites and genotypes.

Table 11.3 Increment in aboveground biomass and in the N and K accumulation in *Eucalyptus grandis* and *Eucalyptus urophylla* from age 2–4 yr (Pereira 1990)

Age (months)	Biomass (t ha^{-1} yr^{-1})		N (kg ha^{-1})		K (kg ha^{-1})	
	E. grandis	*E. urophylla*	*E. grandis*	*E. urophylla*	*E. grandis*	*E. urophylla*
0-24	13.9	13.8	117.9	109.2	100.4	122.0
24-30	5.8	5.3	30.0	41.7	13.8	28.5
30-36	8.4	8.4	27.3	31.4	24.3	45.0
36-42	9.3	8.6	8.0	16.8	2.7	8.2
42-48	21.3	21.4	30.3	62.4	17.1	27.8
Total	58.7	57.5	213.5	261.5	158.3	231.5

Responsiveness to fertilizer application at planting time varies among eucalypt species (Barros et al. 1990). In a trial comparing response of eucalypts to fertilisation, the wood volume of 3-yr-old *E. urophylla* and *E. citriodora* increased from 59.9 and 58.2 m^3 ha^{-1} in the control plots, to 88.0 and 63.8 m^3 ha^{-1} respectively, when a complete macronutrient fertilizer was applied. Hence, the former species had a relative growth increase of 47% against 10% of the latter. Recently, Guimarães (1993) evaluated the heritability of P, K, Ca and Mg utilisation efficiency of *E. camaldulensis* and *E. citriodora* progenies in the seedling stage (90 days old), and found significant heritability values varying from 0.38 to 0.91. The highest values were for Ca and Mg.

Constraints on Production

Management practices for achieving high production of fast-growing, short-rotation crops offer economic return, but are accompanied by risks. Some of the risks highlighted in other chapters can be severe (e.g. see Chapter 10) if management practices are applied with poor understanding of the ecosystem processes and their relationship to long-term productivity. In the following account we have addressed four common constraints on production and describe how they can be overcome by management.

Soil compaction

Forest operations, especially harvesting, if carried out without due care of soil properties can cause several types of soil damage including soil compaction (Sim and Nykvist 1991; Lacey 1993; Costantini 1995). Tree growth can be impaired in soils with high bulk density because high soil strength restricts root growth, and hence reduces nutrient uptake and reduces access to stored water. High bulk density also lowers soil porosity. In some tropical soils which have high P-fixing capacity, a degree of compaction may enhance P adsorption by reducing the distance between adsorbing surfaces and P in the soil solution (R.F. Novais, unpublished). Several studies with seedlings under glasshouse conditions have shown a marked reduction in growth as soil bulk density increased. The increase of the bulk-density of a clayey soil from 0.90 to 1.30 g cm^{-3} significantly reduced the height of *E. grandis* seedlings and their P content; the reduction in growth was partly overcome by adding high rates of P to the soil (Ribeiro et al. 1987). High soil compaction is likely to have greater effect on tree growth during drought periods because it reduces water availability.

Impacts of forest management on soil properties occur unevenly throughout the operational area, a feature that can make the assessment of effects of compaction on stand productivity difficult (Nambiar 1996). M.M. Ferreira (pers. comm. 1993) conducted a field survey in the savanna areas of the Central region of Brazil where the dry season lasts from 3 to 5 months and examined the relationship between natural variation in bulk density of Inceptisols and growth of 4-yr-old *E. camaldulensis* stands. Planting and stand management techniques applied were the same throughout the surveyed areas. The measurement plots were randomly distributed in each stand. Data from measurement plots were grouped into four classes and are presented in relation to the mean bulk density data for the respective group (Table 11.4). The stem volume decreased sharply with increased soil bulk density, falling from about 90 m^3 ha^{-1} to 25 m^3 ha^{-1} as the surface soil density increased from 1.06 to 1.26 g cm^{-3}. Such unevenness in stand growth at a site is undesirable for making decisions on stand management. Subsoiling or ripping such soils may improve tree growth because a larger volume of soil can be explored for water and nutrients. In South Africa, Gardiner (1991) reported that subsoiling to 1.2 m depth combined with contour bench terraces or mounds significantly increased the water-holding capacity of shallow soils (Lithosols) leading to gains in *E. grandis* height growth of up to 49% as compared with planting in pits, 11 months after planting. Subsoils with high strength can severely affect tree growth primarily by reducing the rooting volume. However, a relatively small area of low penetration strength (e.g. natural faults) and old root channels can provide a surprising degree of access for root growth to lower parts of the profile and hence greater access to water (Nambiar and Sands 1992).

Poor harvesting and subsequent site management practices can adversely affect productivity in tropical plantations (Sim and Nykvist 1991; Panitz and Yaacob 1992). In areas that have been logged with mechanised timber extraction, soil compaction is a common problem on snig tracks. In Malaysia, Malmer and Grip (1990) found that skid trails covered 24% of the area if logs were mechanically extracted, but only 4% if the harvest was manual. After timber extraction by machinery, soil density of the top 5 cm of a clayey soil increased from 0.82 to 1.28 g cm^{-3}, and the steady state infiltration rate decreased from 37 mm hr^{-1} to 0.28 mm hr^{-1}. Under such conditions, scarifying or ripping the tracks helps to restore infiltration capacity. The long-term effect of physical damage to soil at a field operational level on stand productivity has not been properly assessed and warrants much further work including different soils, their condition, slope of the land and the type of harvesting operations. Given the increasing degree mechanisation and the expansion of plantation area to marginal and degraded soils the knowledge from such studies would have considerable pay-back.

Table 11.4 Variation in stem volume growth between plots in a *Eucalyptus camaldulensis* stand growing on an Inceptisol of Brazilian savanna and the soil bulk density in those plots (adapted from Pereira 1990)

Plots	Soil bulk density (g cm^{-3})		Stem volume
	0–20 cm	20–40 cm	(m^3 ha^{-1})
1	1.26	1.23	24.7
2	1.14	1.18	39.3
3	1.13	1.24	63.3
4	1.06	1.18	89.7

Impacts of harvesting on nutrient capital

Harvesting high-yielding plantations imposes a direct drain on nutrient capital by removing nutrients in the harvested tree components. Losses may also occur through leaching, erosion and volatilisation. Even if only the stem is harvested the amount of nutrients removed can be high, especially by repeated harvesting of short-rotation crops (see Chapter 10). These losses are likely to be enhanced by faster organic matter decomposition at the exposed sites. As noted earlier, soil compaction due to harvesting and other site disturbances can induce erosion and reduce the accessibility of nutrients to roots. Slash burning would lead to net loss of nutrients especially N. Soil preparation for planting also influences nutrient dynamics.

Although a close correlation is found between yield and nutrient uptake (Fig. 11.3), there is large variation in the amount of nutrient removed because of differences in soil nutrient availability, nutritional requirement or content of species, stand age and in harvesting practices. Table 11.5 summarises data for the nutrient content of stem wood and bark in several species across a range of stand ages and sites (see also Chapter 10). The striking feature of the data (Table 11.5) is the very wide range in nutrient content reported in different studies. Such variation precludes the possibility of drawing any general conclusion about the rate at which individual nutrients may be removed by wood harvest. The wide variation is due to numerous reasons including differences in sampling techniques, analysis and methods of calculation. Some results appear to be much higher than the commonly-found range, for example the results for the 18-yr-old *Tectona* stand in Nigeria. For the data from Brazil where the methodology of measurements is comparable, it can be concluded that nutrient removal by harvest would be closely related to the wood yield obtained. Debarking in the field and removing only the stemwood minimises nutrient depletion. For short-rotation eucalypts, on average 10%, 30%, 25% and 30% of N, P, K and Ca of the aboveground portion of the tree are held in the bark (Gonçalves 1995a; see also Chapter 10). Very few studies have related the amount of nutrients removed in harvests with the total and available pools of nutrients.

Additional amounts of nutrients will be lost from the site if the slash and the forest floor are burned. In Brazil, the nutrient content of the canopy of eucalypt stands near rotation age (7–8 yr) represents about 30% of that in the aboveground biomass, except for Ca, of which the highest proportion is contained in the bark. Litterfall, for different site conditions and stand ages from 3 to 8 yr, returns 4 to 8 t ha^{-1} of dry matter every year, containing from 19 to 52 kg $ha^{-1}$of N, 1 to 3 kg ha^{-1} of P; 3 to 12 kg $ha^{-1}$of K and 11 to 32 kg ha^{-1} of Ca (Reis and Barros 1990). Values for litterfall and nutrients in the same range were reported by Bargali et al. (1992a) in an age sequence of *E. tereticornis* in India. The rate of litter production is a function of growth rate, and the reported amounts of litter accumulated on the forest floor are quite variable (see Chapter 13). Wang et al. (1991) detected 6.5 to 16 t ha^{-1} of litter under plantations, 5.5 yr old, of four broadleaf species growing in Puerto Rico. Under these conditions the amount of N varied from 100 to 256 kg ha^{-1}, of K from 11 to 18 kg ha^{-1} and of Ca from 45 to 150 kg ha^{-1}. Burning these residues may lead to significant losses of nutrient by volatilisation, leaching and erosion. In the savanna

Table 11.5 Amounts of nutrients in stem wood and bark of several species cultivated in tropical plantations

Genus/Species	Location	Stand	Wood	Nutrient in the stem (kg ha^{-1})				Reference
		Age (yr)	Yield (t ha^{-1})	N	P	K	Ca	
Eucalyptus	Brazil	8	43–390	78–800	4–40	32–554	43–686	Reis and Barros (1990)
E. grandis	S. Africa	7	75–200	80–204	7–15	131–324	164–400	Herbert and Robertson (1991)
E. tereticornis	India	8	65	64	6	69		Bargali et al. (1992a,b)
Pinus patula	Swaziland	17	166	204	33	127	130	Morris (1992)
Pinus oocarpa	Brazil	9–14	102–112	132–203	10–17	42–87	54–79	Barros (unpublished); Poggiani (1985)
Pinus caribaea	Nigeria	10	97	196	10	76	84	Egunjobi and Bada (1979)
P. caribaea	Brazil	9–11	99–161	160–402	17–32	61–96	55–192	Barros (unpublished); Russel (1983)
Terminalia	Nigeria	13	108	422	5	469	129	Ola-Adams (1993)
Tectona	Nigeria	18	350	1677	27	1680	687	Ola-Adams (1993)
Casuarina	Puerto Rico	55	153	203	65	92	490	Wang et al. (1991)
Stryphnodendron	Costa Rica	4	55	270	38	110	445	Montagnini and Sancho (1994)
Vochysia	Costa Rica	4	55	143	38	231	803	Montagnini and Sancho (1994)

region of Brazil, burning the slash (leaves and small branches) of the natural vegetation led to losses to the atmosphere of 88% of N, 33% of P, 30% of K and 47% of Ca (J.L.P. Maluf, pers. comm. 1991).

Nutrient losses by leaching and soil erosion

Studies quantifying nutrient losses by leaching and erosion in tropical and subtropical planted forests are scarce. Nutrient losses by these two processes are expected to be greatest during harvesting operations, site preparation and slash burning. Nutrient leaching is unlikely to be important in established forest because there is seldom deep drainage and much of the water infiltrating the soil is used by the stand. Smethurst and Nambiar (1990b) found that in a *Pinus radiata* plantation on podzolised sandy soil close to clear-falling the rate of N mineralisation was equal to rate of uptake and hence there was no leaching. In the Jari project in the Amazon, with annual rainfall of 2300 mm and temperature varying from 18 to 25°C, the conversion (selective logging of 60% of the timber, and burning of slash and remaining forest) of a native forest (541 t ha^{-1} of biomass) growing on a sandy Ultisol, to a plantation of pine or *Gmelina*, resulted in leaching losses of 200 kg ha^{-1} of K (corresponding to 19% of the initial capital), 100 kg of Ca (7% of the initial capital) and 140 kg of Mg (20% of the initial capital) (Russel 1983). Information on potential nutrient losses due to leaching and erosion under different plantation forestry management practices needs to be obtained for specific ecosystems.

In general, the loss of soil, organic matter and nutrients is closely related to the degree of site disturbance, the rainfall regime and the slope. In south-eastern Brazil, losses by conversion of secondary forest to maize plantation (yellow Latosol, 14% slope, 1240 mm yr^{-1} rainfall) varied widely depending on the site preparation practices (windrowing, broadcast burning or stump raking): for example, soil erosion 0.13–1.89 t ha^{-1} yr^{-1} and Ca loss 2.9–12.0 kg ha^{-1} yr^{-1}. Several factors including the amount of runoff, the size of the pool of nutrients and the rate of mobilisation of organic matter influence the nature and extent of loss.

In a study in Malaysia, Malmer (1993) reported significant increases in runoff, suspended soil and nutrients in the stream water due to land preparation (Table 11.6). Slopes in the area were moderate, ranging up to 27%, and the soils were an Orthic Acrisol and Gleyic Podzol. The mean rainfall during the assessment period was 3804 mm yr^{-1}. The treatment involving log extraction by tractor (W-5) caused the largest losses of soil and nutrients, particularly of K. Leaving the slash in the area (treatment W-4) reduced runoff as compared to plots where the slash was burned.

Clearly, many of the losses indicated here and elsewhere (Chapter 10) can be substantially reduced by appropriate site management practices.

Table 11.6 Increases in runoff, suspended soil and dissolved nutrients in the stream-water of watersheds in Malaysia, as influenced by the method of land preparation (adapted from Malmer 1993). Observations were made over periods of up to 33 months following the commencement of operations.

Treatment*	Runoff mm yr^{-1}	Suspended soil (t ha^{-1} yr^{-1})	Dissolved elements (kg ha^{-1} yr^{-1})					
			N	P	K	Ca	Mg	C
W-1	336	0.13	6.2	0.03	27.7	9.3	1.7	42.9
W-4	149	0.70	9.8	0.10	34.9	8.2	2.5	65.4
W-5	397	2.40	13.1	0.20	62.5	8.8	5.1	55.4

*W-1: Clearing of secondary vegetation in 1987 (following selective logging of dipterocarp rainforest in 1981 and wildfire in 1982/83), burning and planting.

W-4: Clearfelling in 1987 (following light selective logging of dipterocarp rainforest in 1981), manual extraction of logs, no-burning and planting.

W-5: Clearfelling in 1987 (following light selective logging of dipterocarp rainforest in 1981), crawler tractor extraction of logs, burning and planting.

Competition for water and nutrients

Fertilisation can enhance growth of competing and understorey vegetation which can limit the growth response of plantation trees to fertilisation because of competition for site resources i.e. water, light or nutrients. Nambiar and Sands (1993) provided a synthesis of the competition processes determining water and nutrient availability in plantation forests. Where these site resources are likely to become limiting to growth, strong interactions between vegetation control and fertilisation are observed. On soils with large seasonal variation in water supply, heavy weed infestation in stands with open canopies will reduce the effects of the fertilisation, especially by reducing water availability to the trees. However, Sands and Nambiar (1984) found during successive summer periods that the effect of weeds on tree water status diminished as tree roots increased their access to water stored deeper in the soil profile. Woods et al. (1992) showed in a *Pinus radiata* plantation between two and three yr of age, weeds increased the uptake of fertilizer N by plant biomass and thus N retention on site, reducing N leaching. They also demonstrated that when N is plentiful, intensive weed control is unnecessary in plantations beyond two yr of age, and vice-versa when the N soil levels were low. On the other hand a continuous crown cover as encouraged by fertilising mainly during the first 12 months (Cromer and Williams 1982; Cromer et al. 1993) helps to shade out and suppress competition from weeds.

The level of intensity of vegetation control needs to be established with a sound understanding of competition processes (Woods et al. 1992; Nambiar and Sands 1993). Depending on site conditions and land preparation methods, complete weed elimination may not be desirable for conserving nutrients. Lowery et al. (1993) reviewed information on weed control in tropical forest plantations and concluded that although complete weeding in most cases resulted in best growth and survival, partial weeding in strips along the tree rows may represent a good compromise between making soil resources available to the crop trees and nutrient conservation on the site (see also Woods et al. 1992). A critical requirement is to define how long tree seedlings and weeds can grow together before survival and growth of the trees is threatened. In an area infested by *Panicum maximum* in south-eastern Brazil, Marchi et al. (1995) found a continuous decrease in volume growth and an increase in mortality of *Eucalyptus grandis* as the period of competition (delay in number of days from planting to application of weed control) increased (Fig. 11.5). Weed management is most critical during the weeks or months immediately after planting depending on the nature of water availability (Lowrey et al. 1993; Nambiar and Sands 1993). Judicious management of vegetation using mechanical or chemical means is a fundamental requirement for the successful establishment and development of commercial plantations.

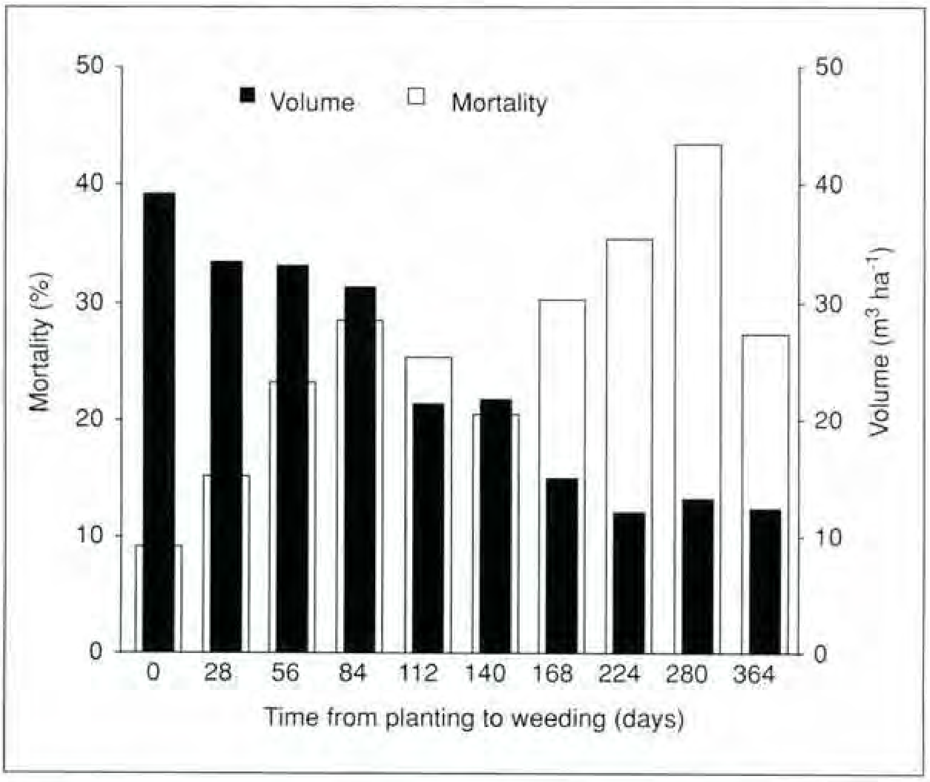

Figure 11.5 Mortality and stem volume of *Eucalyptus grandis*, 22-months-old, as affected by weed competition. (Adapted from Marchi et al. 1995)

Nutrient Amendments and Correction of Nutrient Deficiency

The application of fertilizers is not yet a widespread practice in plantation forestry in subtropical and tropical areas but it is steadily increasing. Fertilizers have been used in conifer plantations in temperate plantation forestry for many decades, often with spectacular benefit (Ballard 1984). Routine application of fertilizers is common in plantations of fast-growing species in Australia, New Zealand, South Africa, Chile, southern USA and Brazil. Indeed, successful plantation forestry would not have been possible in large areas of these countries without the use of fertilizers. The most common nutrient deficiencies in the temperate region that have needed correction are P, N, Zn, Cu and B. Many of these deficiencies are also occurring in subtropical and tropical forestry.

The extent to which fertilizer application to plantations may become common in the developing countries of the subtropics and tropics depends on many social and economic considerations outside the scope of this chapter. In Brazil, where plantation development is driven by the commercial considerations of an internationally-competitive wood-based industry, application of fertilizer and other intensive management practices are recognised as economically rewarding and hence a common practice. The principle underlying these practices and experience of their application in the Brazilian context are discussed below to highlight some of the key aspects of nutrient management for short-rotation forestry on soils with relatively small nutrient reserves.

Diagnosis of nutrient requirements

The diagnosis of nutritional status and fertilizer recommendations have commonly been based on the nutrient concentration in topsoil and in foliar tissues. Sometimes visual symptoms are so distinctive that a useful conclusion regarding nutrient status can be drawn from visual inspection (Dell et al. 1995). Although it is important to know in the first instance which nutrient or nutrients are limiting growth (a qualitative appraisal), more often it is important to know how severe a deficiency is and also to be able to predict the response to given quantities of fertilizer applied to particular sites. Our field experience shows that for macronutrients, the order of the reliability of visual symptoms of deficiency in eucalypt and pine plantations to make decisions on fertilizer application is in the order: $P > N \geq K \geq Ca > S > Mg$. For micronutrients the sequence appears to be $B \geq Zn > Cu$.

The main limitation of soil and tissue analysis is that estimated nutrient status may not parallel the developmental stage and nutritional demand of trees, particularly when the stands have reached a phase when nutrient cycling has become an important process. This may result in an imprecise evaluation of nutrient status of the trees and consequently inefficient fertilizer recommendations. Rooting depth is also important, as it influences the total volume of soil available for exploitation of both nutrients and moisture. The nutrients in the 0–20 cm layer of soil layer are related with tree growth in short-rotation forestry (Gonçalves et al. 1990). In this layer absorption of nutrients by fine roots is most active. However, to obtain an idea of the chemical and physical limitations to root activity at depth, soil samples from the 20–40 cm and/or 40–60 cm layers, depending on soil profile homogeneity, should also be analysed (see Chapter 10).

Foliar analysis is a good indicator of nutritional stress in many species, especially if vigorously and poorly growing trees are compared (Mead 1984). This technique is particularly suitable in plantation forestry in combination, where possible, with soil analysis and fertilizer trials (Herbert 1991). Good relationships have been established for young stands of *Eucalyptus grandis* between foliar nutrients, growth rate and responses to fertilisation at planting (Schönau and Herbert 1983). Herbert (1991) found that 78% to 96% of the variation in foliar nutrients was explained by multiple regressions involving site and soil parameters. However, the ratios between N, P, K, Ca and Mg are of more use as a diagnostic tool in examining the nutrient status than are critical foliar values for individual elements. The Diagnosis and Recommendation Integrated System (DRIS) has been useful in explaining variation in growth (Sumner 1990), especially where soil fertility is sufficient to allow reasonable growth rates (Herbert and Shönau 1990).

Techniques for diagnosis of nutrient deficiencies have progressed over the past thirty yr, allowing the forest manager to be confident that nutrient deficiencies can usually be detected and that, in many cases, growth on unfertilised sites can be predicted. However, diagnostic techniques to assess nutrient status and to predict the magnitude of response to fertilizer (especially in the absence of conspicuous deficiency) for advanced management planning still require continued research.

Application of fertilizers in relation to stand development

Fertilizer application may be needed because the soil is not always able to supply all the nutrients that plants require for sustained growth. This can happen either because of inherent deficiency or nutrient loss. Even on some fertile soils growth can often be increased by fertilisation with one or more nutrients, the outcome depending on species nutritional requirements, soil moisture and nutrient availability, and silvicultural practice. Fertilizer application is the simplest way of improving the fertility of soils, and there is clear evidence of successful use of fertilizer to increase commercial productivity in tropical and subtropical regions (Herbert and Schönau 1989, 1990; Barros et al. 1990; Cromer et al. 1993; Gonçalves 1995b). In the savanna soils in Brazil, fertilizer application is essential to increase and to maintain productivity.

If the loss of nutrients by harvest of short-rotation plantations is high and beyond the natural replenishing capacity of the soil, repeated fertilizer applications will be necessary to sustain productivity and to ensure a steady rate of wood supply to industry. In a low-fertility Oxisol of the savanna area in Brazil, stemwood production of *E. grandis*, at age of 8 yr, increased from 55 t ha^{-1} to 125 t ha^{-1} with the application of 100 kg K ha^{-1} at the time of planting the first rotation (1R) (Fig. 11.6). A partial K-balance sheet for soil, estimated at the beginning of the second crop, and the relationship between soil K and growth established in a separate study, indicated a possible reduction in yield (estimated only) in the second rotation (2R) because of insufficient K supply, even in the plots where 200 kg ha^{-1} of K had been applied in the first rotation (Fig. 11.6).

Although the concepts of three stages of stand development proposed by Miller (1984) are useful in relation to long-term slow-growing plantations, in intensively managed short-rotation cropping we may focus for practical purposes on two stages (before and after the first closure of the canopy) (Herbert and Schönau 1989; Gonçalves 1995b). Nambiar (1990) examined the interplay between nutrients, water, root growth and productivity in young fast growing plantations and described how an understanding of the interaction is important for managing stand nutrition.

Ideally nutrient supply should be matched to nutritional demand for expected growth rate. An important factor determining these processes is the pattern of stand growth and the changes in the rate of growth through different phases (see Chapter 12). Thus, fertilizers are applied in doses split between planting time and the months before canopy closure. This method reduces losses of nutrients by leaching, by immobilisation and, depending on the site, by run-off. The quantity of fertilizer usually applied at planting has a very small effect on the long-term fertility of the soil, but it does supply suitable levels of nutrients to the rooting environment at a stage when the root growth and rooting intensity are being determined. Therefore in nutrient-deficient sites, fertilizer application at planting has a major objective of developing and establishing a vigorous root system, and the resulting beneficial effects on aboveground components can be maintained usually only through subsequent application. Phosphorus and Ca, nutrients that are likely to be depleted in soils typically used for short-rotation plantations, play important roles for root growth during early stand development (Grey et al. 1987; Novais et al. 1990). Regarding Ca, Novais et al. (1990) pointed out that 0.25 $cmol_c$ dm^{-3} of soil was enough to maintain excellent growth rates of shoot and roots of seedlings of *E. grandis*.

Amounts of fertilizer applied in commercial short-rotation forestry vary depending upon the soil, species and silvicultural objectives (Herbert and Shönau 1989; Barros et al. 1990; Gonçalves 1995b). Typical ranges are (kg ha^{-1}): N 30–100; P 30–80 K 30–60; B 0.5–1.0; and Zn 1.0–1.5. In the Brazilian savanna, it has been recommended that 20% to 40% of the N and K, and 100% of the P, be applied at planting. In high P-fixing soils, especially clayey soils, it is useful to apply P in split doses. In general the major responses to fertilizer applied to eucalypts at planting are to P, because most soils in which trees are planted are low in soil P (Herbert and Schönau 1989; Barros et al. 1990; Gonçalves 1995b). Growth response to N is mainly additive (and will not occur if P deficiency is not corrected), depending on the quantity of organic matter in the topsoil and mineralisation rates of N as affected by site preparation practices. Nevertheless, N application was considered important in sandy and shallow soils growing eucalypts in South Africa (Schönau 1983). Small but significant yield increases to additions of K have been found on mesotrophic soils (Schönau 1977), but response to K is much larger in Brazilian savanna (Fig. 11.6). The B supply is particularly important in regions where die-back is common (Savory 1962; Cooling and Jones 1970) and the occurrence of B deficiency seems widespread in recently-established eucalypt plantations (Dell and Malajczuk 1994).

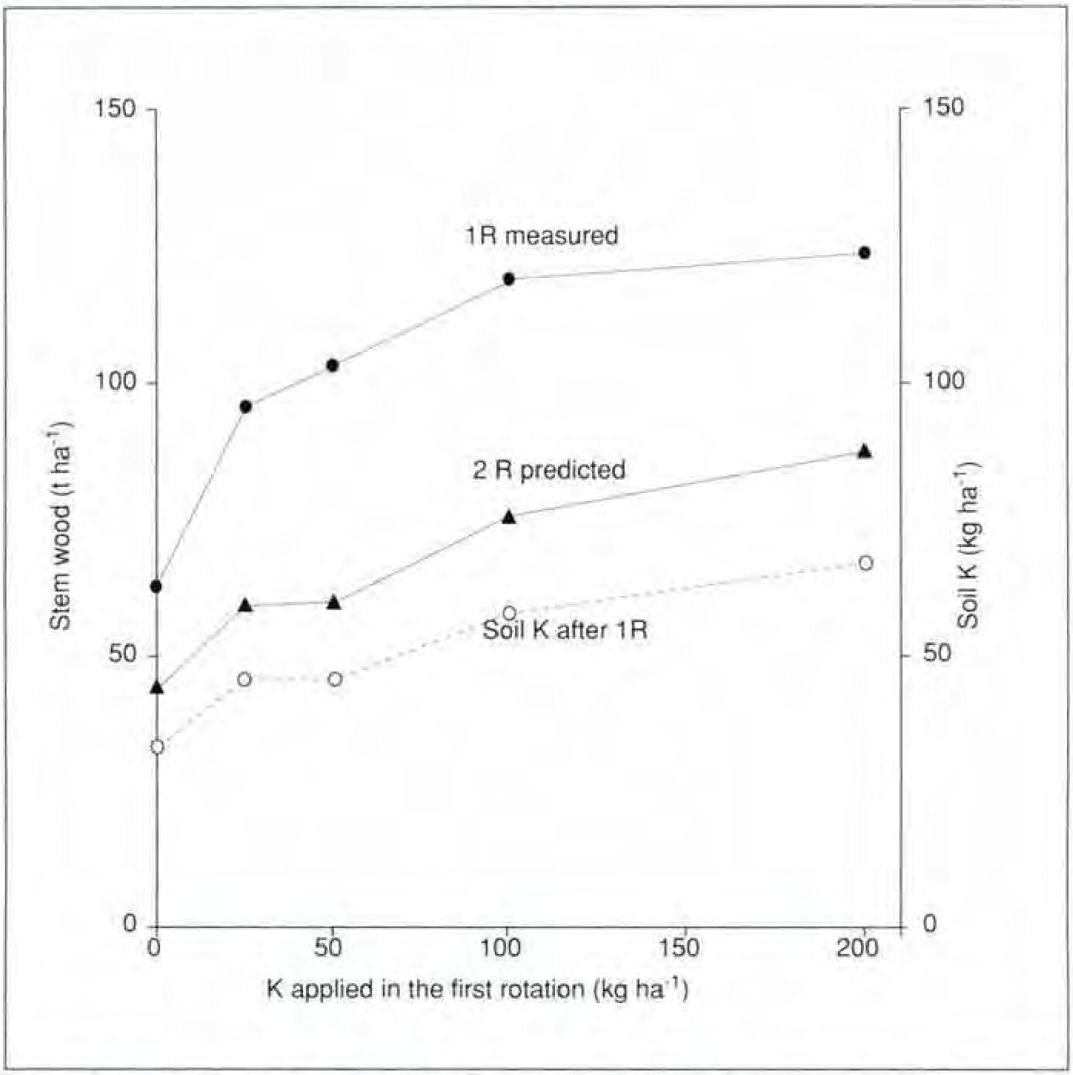

Figure 11.6 Relationship between fertilizer application, residual soil K and stem wood production in the first rotation (1R) and the predicted production in the second rotation (2R) of a *Eucalyptus grandis* plantation on an Oxisol of the savanna region

The benefit from and the technical aspects of localised applications depend on fertilizer solubility and soil reaction. For example, water-soluble P sources should not be mixed with high P-fixing soils but should preferentially be placed (with B if necessary) in the furrows or in planting holes (Barros et al. 1990). Moderately soluble sources such as thermophosphates and partially soluble rock phosphate can be applied in bands, 1.0 to 1.5 m wide, preferably along the planting line. Rock phosphate should be broadcast and incorporated into the topsoil layer on the whole area during soil preparation. When using P fertilizers with low solubility, no more than 30%–50% of the total P dose should be applied in this form. The N, K and P sources can be applied together inside furrows, or mixed with the soil in the planting hole (Gonçalves 1995b). Considering that the concentration of nutrients in soil required for seedling establishment is higher than for growth maintenance, an efficient strategy for improving P nutrition is to combine the application of a water-soluble source of P in spots, in planting holes or even in furrows as starting fertilizer, with banding or broadcasting water-insoluble sources, such as rock phosphate, beyond the establishment phase. This approach was tested by Leal et al. (1988) in *E. grandis* plantations with significant gains in productivity. Fertilising with a soluble source alone or combined with 2 t ha^{-1} of rock phosphate increased volume, at 5 yr of age, to 97 m^3 ha^{-1} or to 182 m^3 ha^{-1}, respectively, compared with 67 m^3 ha^{-1} obtained from the unfertilised plots. It was also found that the application of phosphate rock enhanced Ca and P cycling as indicated by increased concentration of these nutrients in all tree components, including litter. In a clayey soil with high P-fixing capacity, application of 200 kg ha^{-1} of single superphosphate applied in furrows near the planting rows of *E. camaldulensis* resulted in a yield of 98 t ha^{-1} aboveground biomass and 20 kg ha^{-1} P uptake at age 6 yr; in contrast the same amount of fertilizer broadcast and incorporated in the soil (0–20 cm depth) yielded 86 t ha^{-1} of biomass and 15 kg ha^{-1} P uptake (N.F. Barros, unpublished).

The choice of fertilizer source is also a consideration for the nutritional balance in plantations. Primary fertilizer sources (single superphosphate fertilizer) may contain nutrients such as Ca, S, Mg and micronutrients. In some circumstances, the application of lime as a source of Ca may not be necessary when single superphosphate and thermophosphate are used as a source of P. Experimental results from Brazil (Novais et al. 1986; Gonçalves et al. 1989) and South Africa (Herbert 1983; Schönau and Herbert 1983) indicate that the application of lime to correct soil acidity and to neutralise excess Al and Mn is not warranted when planting with species such as eucalypts and pines which are tolerant to low soil pH. Field experience suggests periods of intense rainfall or very dry conditions should be avoided when applying fertilizer.

Nutrient demand varies with stand development and this needs to be recognised in planning fertilizer application. Novais et al. (1986) proposed two sets of critical levels of nutrients in soil as a guide for making decisions on application of fertilizers to eucalypts (Table 11.7). The critical level is defined in this case as soil nutrient content below which there will be a moderate to high chance of response to added fertilizers. The first set (establishment critical levels) refers to levels that allow good seedling establishment in the field (from planting time up to 6–12 months later, depending on site quality under Brazilian conditions). The second set (maintenance critical levels) is the values estimated to be adequate to sustain eucalypt growth from establishment to rotation age of 8 yr. As can be observed in Table 11.7, the critical levels of maintenance increase with site quality, being highest for sites where growth rate is high. These critical levels were developed from many years of experimental data and field experience for *E. grandis* plantations in Brazil and they provide a basis for calibrating other plantation ecosystems where intensive production is planned. However, they should be seen as the best approximations and a guide based on current information.

Table 11.7 Estimated critical soil nutrient levels for the growth of *Eucalyptus grandis* managed on an 8-yr rotation (Novais et al. 1986)

Element	Establishment critical level (0–1yr)	Maintenance critical level (1–8 yr) Volume increment (m^3 ha^{-1} yr^{-1})				
		10	20	30	40	50
P (mg dm^{-3})						
Clay soil	60.00	4.10	4.30	4.30	4.40	4.50
Sandy soil	80.00	6.10	6.20	6.30	6.40	6.50
K (mg dm^{-3})	10.00	30.00	45.00	60.00	75.00	90.00
Ca (cmol$_c$ dm^{-3})	0.20	0.30	0.45	0.60	0.70	0.80
Mg (cmol$_c$ dm^{-3})	0.05	0.07	0.10	0.13	0.16	0.19

Soil sampled in the upper 20 cm; P and K extracted by double-acid extractant; Ca and Mg extracted by 1M KCl

They also show that the amount of fertilizer to be applied to a given species at a particular site will depend on the level of soil fertility and productivity. Nutrient demands of species and rotation length are important considerations for setting critical levels. If information on the type of variables described in this chapter is available, a computer model can be developed to assist operational fertilisation of fast-growing plantations. A preliminary model called NUTRICALC has been developed to estimate nutrient balance and to make fertilizer recommendations for eucalypt plantations in Brazil (Barros et al. 1992).

There are important temporal patterns in nutrient mineralisation and uptake. Smethurst and Nambiar (1990a) showed that following clear-cutting a stand of *Pinus radiata* the amount of mineral N produced during the first 3 yr after planting the next crop is far in excess of the maximum uptake possible. Responses to N fertilisation are unlikely during this stage but may be expected subsequently in soils low in N soil reserves. The rate of N uptake by fast-growing radiata pine increases almost exponentially between planting and canopy closure, from 7 kg N ha^{-1} in the first year to 80 kg N ha^{-1} in the fifth year (Cellier et al. 1985; Nambiar and Bowen 1986), contrasting sharply with the decline in rates of N mineralisation from approximately 45 kg N ha^{-1} in the first year to 20 kg N ha^{-1} in the third year (Smethurst and Nambiar 1990a). Thus an understanding of the synchrony between the pattern of nutrient mineralisation in the soil and the pattern of nutrient uptake by stand is important for managing the nutrition including decisions on fertilizer application.

After canopy closure, nutrients are also cycled through the soil following mineralisation of litter (see O'Connell and Sankaran this volume). At this stage, retranslocation and mineralisation of litter become increasingly important sources of nutrients for growth of new tissues (Nambiar and Fife 1991; Miller 1995). Beyond canopy closure, thinning can create an opportunity for a response to fertilisation as more carbohydrate can be allocated to restore the canopy. Thinning × fertilizer application is not yet a common practice in tropical short-rotation plantations, but forest companies are becoming increasingly interested in thinning eucalypt plantations to grow sawlogs.

Resource conservation

Because many soils under fast-growing plantations in Brazil are low in nutrient reserves including base cations there is a widespread recognition of the need to conserve nutrients at the site and to develop strategies that increase cycling of resources.

Minimum soil cultivation

An ideal management system for plantation forests, as far as nutrition is concerned, would conserve nutrients in the soil and organic matter, releasing them at a rate compatible with the rate of nutrient uptake by the trees and microorganisms, and in such a way that the loss of nutrients is minimised. For conserving water, runoff and soil erosion should be avoided. Stand leaf area should be managed with due regard to water availability and use throughout the rotation (see Chapter 6). The difference between a management system aimed at short-term gain and ideal ones promoting long-term productivity depends on the level of the existing knowledge and the investment of the forest owner in applying the best available knowledge. A combination of knowledge and investment will produce more options for management in the future.

In general, the processes which enhance availability of nutrients also tend to promote nutrient losses from a site. For example, the amount of N leached is directly related to the amount mineralised (Smethurst and Nambiar 1990b). It is common to observe higher early growth rates of trees planted in areas where slash burning was used as compared to trees on unburnt sites. This can be attributed to temporarily increased nutrient availability in the soil of the burnt areas. Zen et al.

(1994) reported gains of 20% and 10% in height of *Eucalyptus grandis* in areas with slash burnt or incorporated in the soil respectively, as compared to where slash was not burned and left on the surface of a Quartz sand soil in south-eastern Brazil. However, no difference between treatments could be observed after 6.6 yr. An alternative method (named 'minimum soil cultivation') to avoid the detrimental effects of burning and of intensive soil preparation has been adopted in Brazil, especially for areas to be replanted (second or third rotation). Basically it involves the retention of slash of the previous crop in rows, debarking at the site and distributing bark in between rows, and no burning. Seedlings are planted by hand or in machine-made pits or furrows (about 20 cm wide and 40 cm deep) opened by a one-tine ripper. Fertilizers are applied in the pit or in the furrow. If grass is the main competing weed, pre- and post-emergence herbicides are applied on the planting rows at the outset. Early results from trials show that this minimum disturbance approach resulted in a higher volume of *E. grandis* than did the intensive preparation (slash burning plus discing), in one case the differences between treatments being 27.5% at age two yr and of 6.5% at six yr. Long-term studies to examine the effect of harvesting and site preparation practices on critical soil process and stand growth are in progress. Substantial increase in productivity due to retention of slash has been found in several second-rotation sites planted with *Pinus radiata* in Australia (Borschmann 1995).

Recycling through organic waste and ash

A source of nutrients, important both silviculturally and environmentally, is residues from the wood-based industry. This option extends the concept of nutrient cycling traditionally described within a forest ecosystem. There is widespread interest in returning residues from the mill to the growing site, and a considerable amount of research is now under way. This approach has a dual benefit of avoiding or minimising the environmental problems of disposing of forest industrial waste as well as improving productivity of plantations.

Several sources and practices are being developed and applied: sources included municipal and other organic waste, pulpmill solid waste as composted at the site, and ash produced by pulpmills which obtain a part of their energy requirement by burning biomass harvested from plantations.

Encouraged by the substantial growth gain achieved in field trials, some companies are applying sludge, with no subsequent treatment, directly from the pulp industry to the field. Fabres et al. (1994) found that the height of *E. grandis* was increased by 68% by applying 60 m^3 ha^{-1} of sludge (11% suspended material) to new plantings during the establishment period. The sludge suspension is a means of applying water to young plantations and can be enriched with nutrients if necessary.

The use of organic waste is promising for plantation areas near large cities where municipal garbage is available in large quantities. Zen et al. (1994) studied the effect of applying municipal compost between tree rows on the growth of *E. grandis* on a poor Quartz sand soil (96% sand, less than 9% of base saturation and CEC of 1.8 $\text{cmol}_c\ \text{kg}^{-1}$) (Table 11.8). Application of increasing rates of compost gave volume increases ranging from 32% to 58% . The composition of the compost was N 1.8%, P 0.23%, K 0.89%, Ca 2.11%, Mg 0.30% and C:N ratio 16. Under some conditions application of compost increased tree growth by improving soil moisture retention and nutrient availability.

Table 11.8 Stem volume of *Eucalyptus grandis*, 4-yr-old, following application of compost made from municipal garbage (adapted from Zen et al. 1994)

Compost (t ha^{-1})	Volume ($m^3\ ha^{-1}$)
0	116
7	118
14	135
21	155
28	154

In the savanna area in Brazil the application of 2 t ha^{-1} of slag from the steel industry, which uses charcoal (produced from plantation grown wood) in smelting, increased the volume of *E. camaldulensis* from 43 to 56 $m^3\ ha^{-1}$ at an age of 6 yr. The slag used is rich in Ca (33%) and Mg (3.4%) (Oliveira et al. 1994).

Application of ash is another common practice to return nutrients to sites (Gonçalves and Moro 1995). Ash (containing 4.7% Ca and 1.4% Mg) obtained from burning biomass (mostly stem bark), applied at rate of 5 t ha^{-1}, increased the volume of a 6-yr-old *E. grandis* stand, growing on sandy soil in the south-east region of Brazil, from 38 to 86 $m^3\ ha^{-1}$ (Benedetti 1994).

In another study (Moro and Gonçalves 1995), ash was applied to beds prepared for planting and was incorporated in the surface soil (0–10 cm) layer. Treatments included several levels of ash and for comparison a fertilizer treatment. The positive effect of ash on the growth of *E. grandis* at age 79 months is shown in Table 11.9. Maximum growth occurred at an application rate of 20 t ha^{-1}. Addition of ash at even 5 t ha^{-1} gave 71% increase in wood volume, far exceeding the response obtained by a relatively high dose of fertilizer. Application of 417 kg ha^{-1} of 10–20–10 fertilizer produced a volume growth of 219 $m^3\ ha^{-1}$, a 57% increase over control. Ash application improved soil fertility and nutrient uptake by trees, especially Ca and K.

Table 11.9 Effects of biomass ash application on *Eucalyptus grandis* growth at age 79 months in Sao Paulo state, Brazil (adapted from Moro and Gonçalves 1995)

Ash treatment (t ha^{-1})	Stem volume (m^3 ha^{-1})	Growth response (volume increase %)
0 (control)	140	0
5	238	71
10	244	75
15	271	94
20	282	102
25	280	100

Many soils in Brazil supporting plantations are low in available P and exchangeable cations, especially K and Ca. Deficiency of K is beginning to appear in some sites (Fig. 11.6). The often dramatic response to compost and ash application has given much impetus to conservation and resource recycling approaches in forestry.

Synthesis

In tropical plantations, nutrients and water are the two main factors defining productivity. Hence sound management practices for the soil and stand are of paramount importance for improving and sustaining productivity. There are a number of risks associated with intensive, short-rotation, high yielding forestry in the tropics. Those risks must be carefully assessed and managed.

Short-rotation plantations of fast-growing species managed as successive crops accumulate large amounts of nutrients within short periods. The long-term productivity of such a system would require judicious application of fertilizer, which under Brazilian conditions of forestry business is a profitable practice. There is a considerable amount of information on the use of fertilizers, especially for eucalypts and pine. However, fundamental studies are necessary on nutrient cycling and the fate of nutrients in tropical plantation forests. Understanding how soil properties influence water and nutrient uptake by trees grown under a range of management practices will help to develop environmentally sound techniques to improve both water and nutrient use by the forest. More fundamental research is also needed to understand the behaviour of the selected genotypes in terms of nutrition and water-relations, given the range of silvicultural practices which may be used.

Most forest owners pursue high productivity by using the best available genetic material and soil and stand management practices based upon empirical information and practical experience. The Brazilian experience has shown that despite repeated short-rotation cropping (two to three cycles in most cases), continuous gains in productivity of eucalypts and pines are possible. It has been estimated (ABECEL 1995) that using the area under plantation as a whole the average wood yield has increased from 30 m^3 ha^{-1} yr^{-1} in 1980 to 42 m^3 ha^{-1} yr^{-1} in 1995. The corresponding pulp yield has been increased from 5.7 t ha^{-1} yr^{-1} in 1980 to 10 t ha^{-1} yr^{-1} in 1995. The rate of increase has been steady over the 15 yr, indicating the large-scale productivity gain through improved genotype and silviculture.

Fundamental studies on the dynamics of organic matter over repeated crop cycles, using both experimental and modelling approaches, need to be commenced as a priority; knowledge from such research will assist the development of sustainable management practices. 'Minimum soil cultivation' as a practice for inter-rotation management is a new and promising option that should be studied in depth.

Plantations forests as an economic activity have to compete with alternative land uses. The continued success of plantations in the future will depend on forest managers obtaining high productivity of the desired wood quality in an environmentally sound manner. To achieve this goal, long-term integrated studies on the effects of contrasting management practices on soil processes, and how those processes quantitatively relate to stand development and productivity, and impact on the environment, are required. Conservation of maximum amounts of nutrients at the plantation site, and the return of nutrients via compost or ash, deserve continuing research and application.

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12

Stand Development and Productivity

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Abstract

Productivity of tropical plantations varies widely, depending on site resources and species. The high growth rates achieved in some cases result from plentiful resources (water, nutrients, light), efficient species, favourable environmental conditions, and intensive management to control spacing, genetics and competition. In many situations, however, one or more key resources are scarce and growth is slow. These features affect both the rate of gross primary production (GPP) and the allocation of net primary production (NPP) to stem wood. Relatively small changes in GPP or allocation of NPP can greatly change stem wood production. Stem wood production typically increases in the early stages of plantation development as the leaf area and root-absorbing area of the trees increase. Productivity then peaks and declines; the cause of this decline (while trees are still young and vigorous) remains poorly understood, but it is often associated with declines in stand leaf area and photosynthesis per unit of leaf area. Leaf area and photosynthesis depend very much on the availability of water and nutrients to the stand. The dynamics of leaf and stem growth depend on the density (or spacing) of a plantation, and on the species or combination of species. High stand densities lead to rapid development of leaf area and stem production, but also to small average stem size. Wider spacing lengthens the time required to attain full leaf area and allows more opportunity for competing understorey vegetation to develop but produces larger individual stems. In some cases, mixtures of species may provide greater yields as a result of improved use of site resources, or decreased pest problems. Nutrient cycling differs substantially among species used in tropical plantations; the most widely planted genera (*Pinus* and *Eucalyptus*) produce large volumes of stem wood per unit of nutrient taken up from the soil. These species also return small amounts of nutrients in litterfall compared to some other genera and to natural forests, which may have implications for sustained nutrient cycling. We stress that the combination of factors that underlie the productivity of tropical plantations is very responsive to management activity. For example, an optimal fertilisation regime should result not only in higher rates of stem growth but will also affect the optimal rotation length for maximum economic profitability. The most successful plantation programs will be based on an understanding and integration of the factors that affect stand productivity.

TROPICAL FOREST plantations are among the most productive ecosystems in the world, often exceeding 40 t ha^{-1} yr^{-1} of aboveground net primary production, and 10 t ha^{-1} yr^{-1} of wood production (Lugo et al. 1988). Productivity differs substantially across regions, in response to gradients in water supply, soil fertility, genetics of the trees and site-management practices (Chapter 11). Many tropical sites have supplies of available water and nutrients which lead to much slower growth than the above figures indicate.

These high growth rates offer great opportunities for the production of wood and fibre from tropical forest plantations. A fundamental understanding of stand growth, and the factors that influence it, is vital to achieving and sustaining high rates of plantation production. In this chapter, we review the definitions of productivity, and how productivity is assessed. We examine patterns of stand growth in relation to age, site fertility, stand density and species. We focus particularly on patterns of nutrient cycling in tropical plantations, and conclude with a synthesis of the importance of these factors to sustained productivity of tropical plantations.

Definition and Measurement of Productivity

The productivity of a forest can be viewed from several perspectives. Gross primary productivity (GPP) is the total photosynthesis of a forest, and net primary production (NPP) is the biomass that remains after plant respiration is subtracted. The most common unit for these rates is kg or t ha^{-1} yr^{-1}. Aboveground net primary production (ANPP) omits the productivity of roots and mycorrhizal fungi, and stem wood NPP omits the production of leaves and branches. These components of production accumulate, store and re-translocate different amounts of nutrients and thus influence the dynamic relationship between nutrients, tissue production and rates of photosynthesis.

The accumulation of stem wood is usually the major interest in forestry programs. The current rate of stem wood growth reflects the allocation of GPP to stem wood. Stem wood growth accounts for about 20% of the GPP of a stand, and relatively small changes in GPP (such as a 10% reduction) can amplify to large changes in stem wood growth (such as a 50% decline in growth if the lowered GPP deducts primarily from stem growth). Further, the allocation of carbohydrate to belowground activities (such as root production, maintenance and mycorrhizae) is typically greater than the allocation to wood growth; any changes in allocation pattern (either toward more belowground allocation or less) can result in large changes in stem wood production. The proportion of carbohydrate allocated to belowground production and processes is greatly influenced by stand age, growing environment and management practices that affect the availability of water and nutrients to the stand (Raich and Nadelhoffer 1989; Beets and Whitehead 1996; Ryan et al. 1997; Chapter 8).

In situations where some trees die during a year, the rate of increase in stem wood biomass (stem increment) is less than the stem wood NPP. If large trees die, the death of several trees per ha may match the stem wood NPP of the stand for that year, resulting in no net increase in stem wood biomass despite substantial stem wood NPP. This net increment in stem growth is often expressed as the current annual increment (CAI); the average increment across a given period of stand development is the periodic annual increment (PAI); and the average stem wood production divided by stand age is the mean annual increment (MAI). These stem wood increments can be expressed in terms of basal area (m^2 ha^{-1} yr^{-1}), volume (m^3 ha^{-1} yr^{-1}), or biomass (t ha^{-1} yr^{-1}).

The total amount of living matter at one time is the stand biomass, sometimes referred to as the standing crop. This biomass can be divided into components such as stem wood, merchantable stem wood, branches and foliage. In most forestry studies, biomass is measured in terms of oven dry weight. In some cases, mass is expressed in terms of the carbon content of the biomass (which is typically about half of the total biomass). Estimating carbon content is useful for gauging the flow of carbon through the atmosphere–tree–soil continuum.

The difficulty of measuring each of the production components increases from wood increment to GPP. Stem wood increments are measured as total stem wood basal area, volume, or biomass at two or more points in time; the difference provides the current annual increment, periodic annual increment or mean annual increment per unit of time. Estimates of stem wood volume or biomass are typically obtained from regression equations, where the diameter (or diameter and height) of trees is related to the volume or biomass of the stems.

Stem wood NPP is estimated by two methods. The increments of individual trees (determined from repeated measurements, or reconstructed from increment cores where environmental variation produces an annual ring) may be summed and extrapolated to a hectare basis. Any growth of trees that did not survive to the final measurement is omitted. Since mortality is generally low in forests (< 1%–2% of stems per year in temperate forests; probably 2%–10% in fast-growing tropical forests —Swaine 1994), and because most mortality is often concentrated in slow-growing, suppressed individuals, the underestimation of stem wood NPP by omitting mortality is small when using the individual-tree-increment method.

The error arising from tree mortality is more important when stem growth is estimated from changes in total stand biomass. In this case, the biomass of trees that died during the period must be added to the stem wood increment derived from the change in total stand biomass. The death of large trees removes biomass that accumulated over the life of the stand, which may be large relative to a single year's production. For example, a windstorm killed about 10% of the *Eucalyptus grandis* trees in a 30-month-old plantation in Hawaii (data from T. Schubert, BioEnergy Development Corporation). Based on the increments of the individual surviving trees, the stem production was about 12.6 t ha^{-1} in the subsequent 7 months (=1.8 t ha^{-1} $month^{-1}$). Over this period, stand biomass increased from 45 t ha^{-1} to 52.6 t ha^{-1}, giving a net stem increment of only 1.1 t ha^{-1} $month^{-1}$. To convert this net stand increment of stem wood to stem wood production, the mortality (4.7 t ha^{-1}, or an average of 0.7 t ha^{-1} $month^{-1}$) needs to be added (see Binkley and Arthur 1993 for a more detailed example).

The contribution of branch growth to NPP can be estimated by methods used for stem wood, although the estimation of branch mortality can be more difficult. Leaf NPP is typically estimated from sequential litterfall collections. Total tree ANPP is summed from stem, branch and leaf values. When leaf area is low and substantial light reaches the understorey, the NPP of understorey plants can be a significant portion of the total for the ecosystem.

Belowground NPP is very difficult to measure (see Chapter 8). The increment in large roots can be determined from regression techniques (larger trees have larger biomass in coarse roots), but the production of fine roots may be unrelated to tree size. The major methods include measuring fine root biomass and assuming a longevity value; measuring living and dead fine roots at several points through a season to determine biomass and turnover; and measuring the litterfall and CO_2 respiration from the soil.

The total GPP of forests is more difficult to estimate than NPP. GPP may be estimated by summing NPP with respiration, or may be modelled from various measurements of stands and environmental conditions. Respiration is difficult to estimate accurately, but it probably accounts for half or more of GPP for both temperate and tropical forests (Ryan 1991; Ryan et al. 1994a).

Growth respiration derives from the production of new tissues; maintenance respiration comes from sustaining existing tissues. On an annual basis for fast-growing plantations, each type of respiration may account for about half of the total respiration of trees. Respiration of leaves may be measured as CO_2 efflux in the dark. Respiration of branches and stems can be measured as CO_2 efflux through bark. Respired CO_2 may be 'refixed' through photosynthesis in the bark or leaves, representing an underestimate of true respiration rates (Linder and Troeng 1981). Respiration associated with the growth and maintenance of roots is difficult to estimate; total CO_2 evolution from the soil may be measured and various approaches can be used to separate respiration of roots from respiration of soil microbes (as suggested by Raich and Nadelhoffer 1989). There is large variation in the literature in the proportion of total tree respiration attributed to roots.

Respiration generally increases with temperature, and current models of forest productivity tend to produce proportionally greater predictions of respiration for tropical forests than for temperate forests (cf. Melillo et al. 1993). However, direct estimates of respiration do not always indicate higher relative rates of respiration for tropical forests. For example, Ryan et al. (1994b; M. Ryan pers. comm.) estimated that about 66% of GPP was consumed in respiration for some native forests in Costa Rica; the respiration associated with growth and maintenance of woody tissues was only 8% to 13% (depending on assumptions about scaling of direct measurements). This compares with a reported range of 5% to 13% of GPP allocated to maintenance respiration of stems in temperate and subtropical conifers (Ryan et al. 1995).

Patterns of Stand Growth

The productivity of tropical plantations is very dynamic, showing substantial changes with plantation age, as well as differences that depend on site fertility, stand density and species. Optimal management involves matching species and management practices to site conditions and desired products.

Age

The early growth of plantations typically relates to the timing of deployment of leaf area; production increases directly as leaf area (and light interception). This early phase of plantation development typically lasts from less than 12 months in dense plantations on excellent sites, to several years on poorer sites. At peak leaf area, productivity of the stand may plateau for some period, followed by a substantial decline in growth. The 'classic' pattern of stand growth is illustrated by the growth of *Gmelina arborea* from Jari, Brazil (Fig. 12.1, from Lugo et al. 1988). Data were compiled from hundreds of 0.5-ha plots; the number of available plots declined with age, dropping from over 500 plots in stands less than four yr of age to about 100 by age nine. The mean annual rate of stem wood increment peaked at about age 5 to 7 yr, at a rate of about 5.25 t ha^{-1} yr^{-1}, and declined to less than 5 by age 9 yr. This MAI value would be used to estimate optimal rotation ages, but from an ecological perspective the pattern in current annual increment may be more interesting. The CAI peaked much earlier than the MAI, at about 8 t ha^{-1} yr^{-1} at age 3.5 yr. The decline in CAI was also much more rapid than the decline in MAI. No assessments were made to determine the cause of the decline.

The partitioning of NPP among tree tissues changes with stage of development of the stand. Some forest ecologists have described three stages of stand growth (Attiwill 1979). Initially the majority of NPP is directed at growth of the living biomass, especially development of the tree canopy, and nutrient cycling is dominated by uptake. This is followed by a period when photosynthate is directed primarily to growth of woody tissues and heartwood formation is initiated, and internal redistribution of nutrients becomes important for meeting nutrient requirements for growth. Finally, during the stage of stand maintenance, most NPP is discarded as litterfall and biogeochemical nutrient cycling through decomposition of plant residues becomes increasingly important for tree nutrient supply. What ecophysiological processes produce this pattern? Why does productivity decline after the peak, rather than be sustained at a high level? Surprisingly, these questions have not been addressed adequately by research; the causes of the length of the plateau of maximum production and the size of the subsequent decline remain largely unexplored. Ryan et al. (1997) examined the processes that produce changes in stand production with age. They considered the following possible processes:

- Increasing respiration with accumulation of stand biomass.
- Decreasing nutrient supply with time, leading to greater allocation to root production.
- Reduced photosynthesis owing to increasing resistance to water flow in tall stems.
- Reduced leaf area resulting from abrasion between tall crowns.
- Increased mortality of older trees.
- Physiologic changes associated with 'aging' of tissues.
- Increased reproductive output.

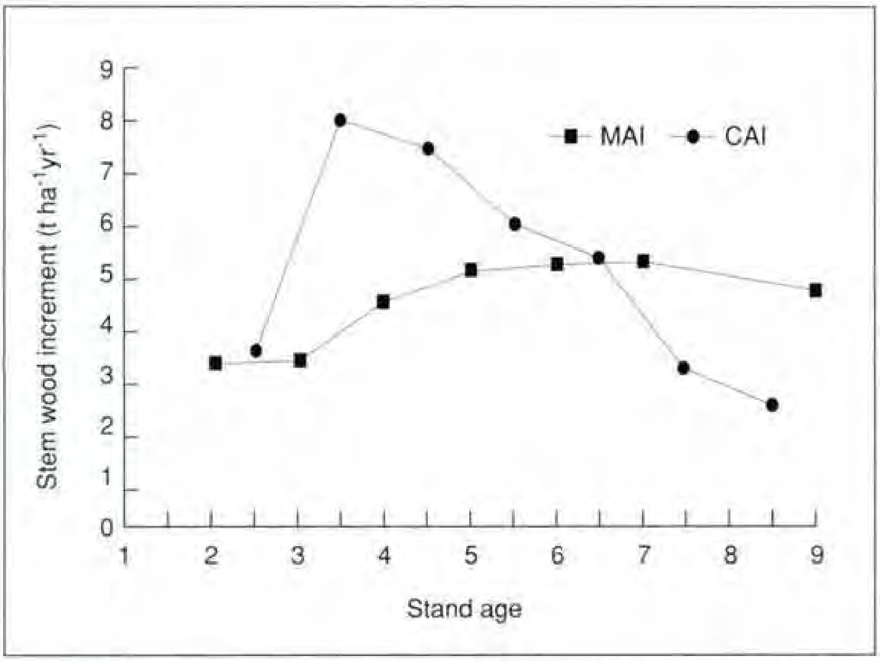

Figure 12.1 Pattern of mean annual increment (MAI) and current annual increment (CAI) for *Gmelina arborea* plantations at Jari, Brazil (data from Lugo et al. 1988)

Discerning the importance of each of the possible explanations is important, because some of the processes, such as changes in nutrient supply, are responsive to management practices. Ryan et al. (1996) concluded that growth declines with stand age represent a 'syndrome' rather than any single process, and key features of the syndrome—declines in leaf area and photosynthetic capacity—appear to be important in most cases.

Some insights are available from two unreplicated age sequences of *Eucalyptus grandis*, one on a fertile soil and another on a poor soil (data from Reis et al. 1985, 1987). On the more fertile site, stem wood biomass exceeded 60 t ha^{-1} after 6 yr, compared with just 24 t ha^{-1} for the poor site (Fig. 12.2). Foliage biomass peaked at about age 3 yr, at 8 t ha^{-1} for the fertile site and 4 t ha^{-1} for the poor site. The efficiency of producing wood per unit of foliage was high at an early age for the fertile site, reaching a peak of about 0.4 t of wood per month for each tonne of foliage. The peak foliage efficiency was about 1/3 lower on the poor site. Both sites declined substantially in foliage efficiency at the same time they declined in foliage biomass. Nutrient concentrations in foliage remained relatively constant across stand ages, so nutrient contents of the canopy (kg ha^{-1}) declined proportionally with foliage mass. The declines in foliage mass, nutrient content of the canopy and the efficiency of producing wood per unit of foliage (or canopy nutrient) suggest two substantial changes over time at both sites. The nutrient supply to the trees probably declined in later stages of stand development, resulting in substantially lower canopy nutrient content. The decline in soil nutrient supplies probably resulted in a greater allocation of biomass to fine root growth at later stages, leading to a lower foliage efficiency of producing wood. For more details on the trends in productivity in relation to stand age and site factors, see Chapter 11).

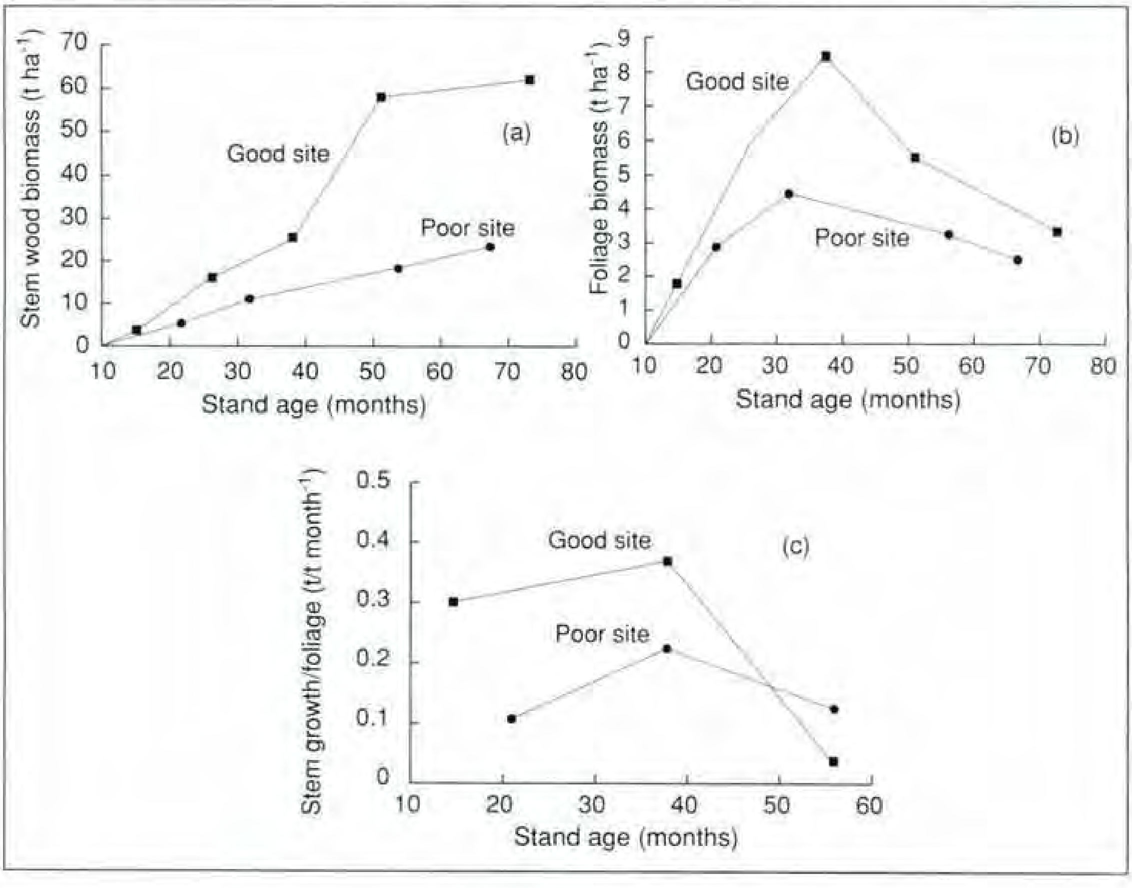

Figure 12.2 Biomass of *Eucalyptus grandis* accumulated much faster on a good soil in Minas Gerais, Brazil than on a poor site. Both sites showed declines in leaf biomass with age, and old stands showed substantially lower efficiency (stem growth/foliage) (data from Reis et al. 1985, 1987)

Similar patterns of ANPP have been reported for an unreplicated age sequence of poplar (*Populus deltoides*) plantations in Tarai Belt of the Himalayas in India (Lodhiyal et al. 1995). The ANPP also increased with plantation age and foliage efficiency (ANPP/foliage mass), which ranged from 1.9 to 2.2 t t^{-1}. An age sequence of *Eucalyptus tereticornis* at the same site (Bargali et al. 1992) showed strong declines in ANPP/foliage biomass with age, but this pattern derived primarily from changes in leaf longevity (total leaf biomass/annual leaf production) rather than from a shift in the ratio between leaf production and whole-tree production. The 2-yr-old plantation carried only 0.5 t ha^{-1} of leaves, with an annual leaf production of 1 t ha^{-1}; older stands retained leaves for more than one year.

These changes associated with stand aging are not apparent in all cases, at least not for traditional rotation lengths. For example, a replicated age sequence of slash pine (*Pinus elliottii*) studied by H. Gholz and colleagues (Gholz and Fisher 1982; Gholz et al. 1986) showed no decline in productivity, nor in stem growth per unit of foliage mass (Fig. 12.3). Stem biomass accumulated most rapidly early in stand development, and showed no sign of slowing through age 34 yr. We omitted from Fig. 12.3 two 34-year-old stands which had substantially less biomass than did the age 26 stands, indicating they were not suitable for inclusion in the chronosequence. Foliage in stands over 14 yr of age produced much more aboveground NPP (per kg of foliage) than in younger stands (Fig. 12.3). Fine root production by the pines increased with stand age, further accentuating the increased efficiency of NPP/foliage biomass in stands older than 14 yr. Inclusion of belowground production would further increase the estimated efficiency of foliage in older stands.

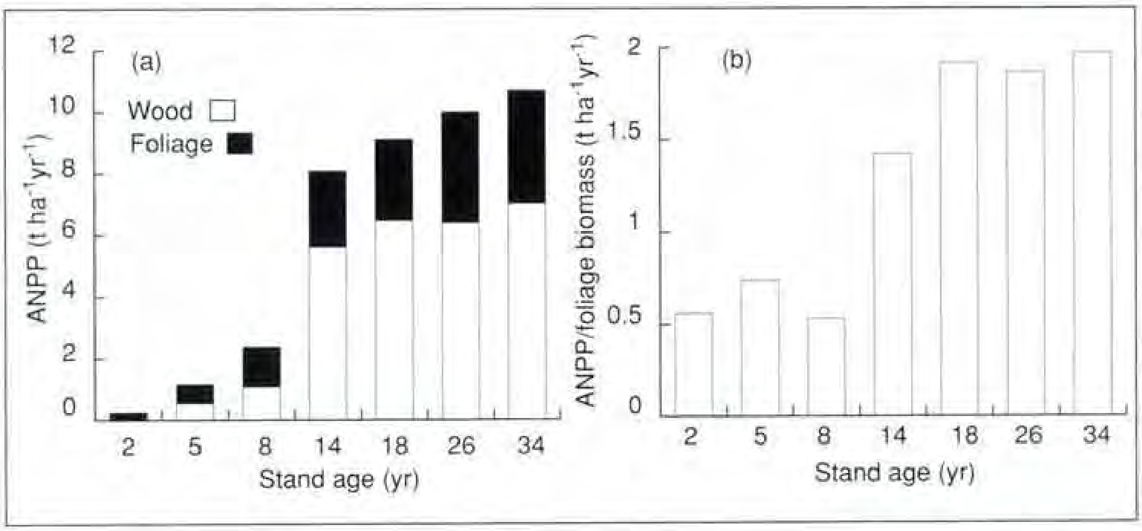

Figure 12.3 Annual production of wood and foliage remained high in older plantations of *Pinus elliottii* in Florida through age 34 yr, and the foliage efficiency (t of ANPP/t foliage) remained high (data from Gholz and Fisher 1982 and Gholz et al. 1986; note that we omitted 2 of their 34-yr-old stands, see text).

Site fertility

Sites that differ substantially in climate, water supply and nutrient supplies will of course differ substantially in stand growth, and in the pattern of stand growth with age (Chapters 6 and 11). Even subtle differences in topography and soils may lead to large differences in resource supplies and stand growth. We expect that sites with plentiful supplies of water and nutrients will allow trees to quickly attain a large leaf area, leading to a rapid peak (or plateau) in growth. This peak should be reached sooner, and be higher, on good sites than on poor sites. Replicated plantations of *Eucalyptus grandis* in Hawaii illustrate this expected pattern. These plantations were established at two sites about 3 km apart under identical plantation conditions (T. Schubert pers. comm.). The same variety of *E. grandis* was planted at each site (in a spacing trial) in the same year. Both sites were on the same soil type, with the same environment (including a year-round growing season, with >4000 mm yr^{-1} of precipitation), but Site 1 had more soil N as a result of land use history. Trees at Site 1 showed faster early growth, with an earlier peak in annual stem wood increment than those at Site 2 (Fig. 12.4). Trees at Site 2 grew more slowly, and took an additional year to peak in growth (a peak that was lower than for Site 2). Interestingly, the productivity of the two sites was more similar in older stages (>4 yr), with the poorer site showing only slightly lower stem increments than the richer site.

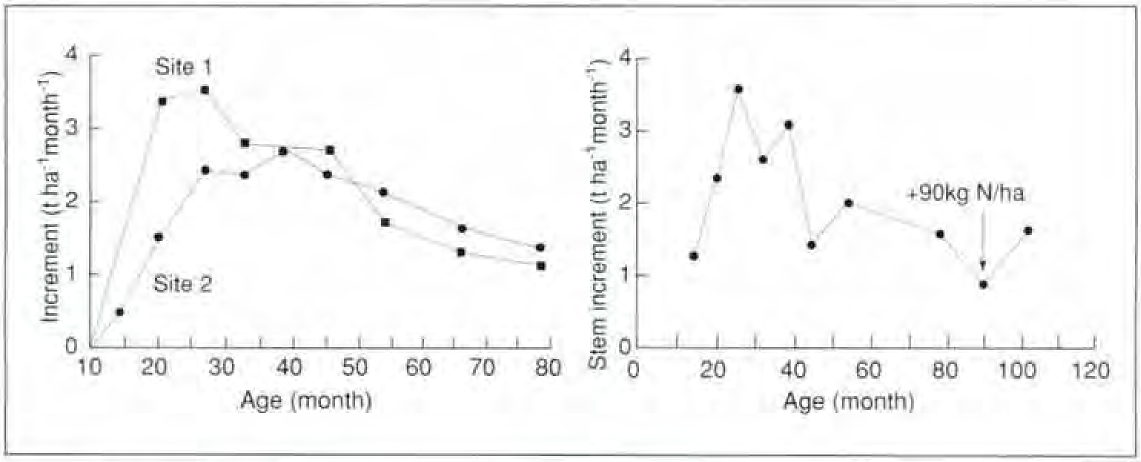

Figure 12.4 Current aboveground increment for *Eucalyptus grandis* on Hawaii peaked sooner and higher at more-fertile Site 1 (both at 0.5 x 3 m spacing), but subsequent declines in growth were similar to those in less-fertile Site 2 (left). A single application of 90 kg N ha^{-1} at 8 yr (at 1 x 3 m spacing) in Site 2 almost doubled aboveground increment (right) (data from T. Schubert, BioEnergy Development Corporation).

What ecophysiological processes account for differences in productivity across sites? Unfortunately, few ecophysiological studies have addressed the processes that underlie differences in stand productivity along gradients in site fertility. In the Hawaii example, Site 1 had greater availability of N and P, and trees had a higher leaf area (Binkley unpublished data), but without information on canopy light interception and photosynthesis, on water relations, or allocation of photosynthate, the contributions of various ecophysiological differences to the difference in stem growth cannot be estimated.

Density

The productivity of tree plantations depends very much on the number of trees per unit area (density or spacing) (Evans 1992). Higher densities typically have greater productivity for a variety of reasons, including more rapid deployment of tree leaf area and root area, reduced competition from non-tree vegetation, and perhaps from canopy structural factors. Unfortunately, ecophysiological studies have not yet produced a clear picture of the relative importance of these factors, or how the factors may vary with site conditions and management activities.

A study with *Eucalyptus tereticornis* in Karnataka, India illustrates a common pattern (Adlard et al. 1992). Tree density ranged from 375 to 30 000 trees ha^{-1} (0.3 to 27 m^2 per tree), and maximum annual increment of 10 to 12 m^3 ha^{-1} yr^{-1} (at age 4 yr) occurred at moderately high densities (2500 to 3000 ha^{-1}). Maximum growth per hectare occurred at high densities and small individual tree sizes. The lowest density produced trees with 3-fold greater diameter than the densities that produced the maximum tree volume per hectare. The optimal spacing of trees depends both on the productivity per hectare and the effect of individual stem size on product values. Kallarackal and Somen (1993) summarised water use and photosynthesis by *E. tereticornis* in Kerala, India. Water use depended heavily on tree density; 1800 stems ha^{-1} led to 1560 mm yr^{-1} of evapotranspiration, compared with just 850 mm yr^{-1} loss when density was 1100 stems ha^{-1}.

Ola-Adams and Egunjobi (1992) examined leaf litterfall in plantations of *Tectona grandis* (teak) and *Terminalia superba* over a 10-fold range of stand densities. Stand density had no apparent effect on litterfall, suggesting no density-related differences in leaf area or production. However, individual tree sizes were much smaller in the high-density stands.

Effects of stand density on competition for site resources (water and nutrients) is also concomitantly influenced by the effect of the density on other vegetation. Eastham and Rose (1990) and Eastham et al. (1990) examined tree × pasture interaction in an agroforestry trial where *E. grandis* was planted at a continuously-varying spacing in a *Setaria*-dominated pasture in a subtropical environment in Australia. They found that tree density affected interspecific and intraspecific competition, altering the distribution of root growth and hence the nature of competition for water and nutrients. As the tree density increased, pasture root growth decreased. Intraspecific competition between trees caused the trees at higher densities to have denser and deeper roots. A larger proportion of the water uptake occurred from deep in the soil profile when the tree densities were higher because of deeper and denser roots under trees and because the water in upper horizons was rapidly depleted.

The effect of tree spacing on nutrient supplies remains largely unexamined, but these effects are probably substantial. For example, Fownes, Ryan and Binkley (unpublished data) found that *Eucalyptus saligna* plantations in Hawaii at 1 × 1 m spacing (10000 stems ha^{-1}) developed a leaf area index of about 4 m^2 m^{-2} by 9 months; plantations at 3 × 3 m spacing (1111 stems ha^{-1}) developed only about half the leaf area by this age. Although both spacing treatments had received substantial fertilisation, the availability of N in the soil was twice as high (based on in-field ion exchange resin bags) in the low-density stand; a high density of trees allowed more complete exploitation of nutrients from both native pools and from fertilizer. Much more work is needed on the interactions between site resources and stand density.

Species

Species clearly differ in ability to grow under specific site conditions. Methods which can integrate information on climate, soil and the ecological requirements of species or provenances, and allow more reliable prediction of the match between trees and sites, are being developed (Booth 1995). Trees do not grow rapidly on stressful sites; they may cope, surviving and growing slowly. Most species grow well on fertile sites provided they are well adapted to the prevailing climate. In general, those species which grow on harsh sites do so by lowering their growth rates. Species that are adapted to stressful sites may depend on their abilities to tolerate stress (such as periodic drought), whereas species that are highly productive on fertile sites may be able to acquire and use resources efficiently. The ecophysiological causes of differences in productivity between species probably include such ability to obtain resources (such as light, water and nutrients), as well as the efficiency of using these resources to produce biomass. An understanding of the ecophysiological basis of differences between species is important for management, because management activities such as weed control and fertilisation can alter supplies of water and nutrients, which may change the ranking of the performance of species. In addition, an understanding of the basis of differences in growth between species could provide insights on the suitability of species for use in mixed plantations.

As an illustration of the differences in productivity with stand age among species, Reddy and Sugur (1992) compared the biomass, mean annual increment and current annual increment (at age 5 yr) for *Acacia auriculiformis*, *Casuarina equisetifolia* and *Dendrocalamus strictus* in Karnataka, India. *Acacia* produced the greatest biomass (and MAI), with 61 t ha^{-1} biomass (12 t ha^{-1} yr^{-1} MAI), and *Casuarina* the lowest (46 t ha^{-1} and 9.3 t ha^{-1} yr^{-1} MAI). However, the current annual increment at age 5 was far greater in the *Dendrocalamus* plots (24 t ha^{-1} yr^{-1}) than in the others (12 to 16 t ha^{-1} yr^{-1}), so *Dendrocalamus* may prove to the be the most productive species in longer rotations. Wang et al. (1991) reported on a similar study in Puerto Rico, with replicated plantations of *Eucalyptus robusta* and nitrogen-fixing *Casuarina equisetifolia*, *Albizia procera* and *Leucaena leucocephala*. At age 5.5 yr, the *Casuarina* had the greatest biomass (199 t ha^{-1} total aboveground), followed by *Albizia* (124 t ha^{-1}), *Eucalyptus* (67 t ha^{-1}) and *Leucaena* (47 t ha^{-1}).

Water use probably differs substantially between species, but few studies have examined water use patterns in replicated species trials. One example comes from India, where Kallarackal (1992) compared water use by fast-growing *Acacia auriculiformis* with *Tectona grandis*. *Acacia* used about 20% more water in evapotranspiration. At a leaf level, *Acacia* lost less water per mol of CO_2 fixed than *Tectona*, but no stand-level comparisons of growth were presented.

Productivity in mixed-species stands

Tree species can be mixed together in plantations when silvicultural objectives can take advantage of differences in the ecophysiology between species. In some cases, both species produce valuable products, and management activities focus on balancing the productivity of both species. In other cases, a primary species may be valued, and the secondary species contribute shade, N (through N-fixation), or protection from insects, pathogens or non-tree vegetation.

Does the productivity of mixtures of species exceed that of monoculture stands? Many agroforestry studies have found that combinations of trees and food or fodder crops can provide greater economic production than monocultures (Vandermeer 1989; Kelty 1992). The yield of mixed-species tree plantations has been debated extensively for temperate forests, with limited insights. In some cases, attempts at mixed-species silviculture have failed (Kenk 1992), owing to poor selection of species or poor management. Other cases where mixtures have appeared more productive than monocultures may have suffered from poor design or analysis. For example, Brown (1992) concluded that inclusion of Scots pine (*Pinus silvestris*) improved the growth of Norway spruce (*Picea abies*) at the Gisburn Forest in England. However, more detailed analysis concluded that pine actually reduced the growth of spruce in these plantations (Yanai 1992). In other situations, competition between species simply results in lower productivity; Turvey et al. (1983) found that naturally occurring wattles (*Acacia* spp.) in plantations of radiata pine lowered pine growth, despite increases in soil N content. The growth of individual dominant trees may be higher in mixtures than in monocultures, as the competitive effects of a small neighbour may be less severe than those of a fast-growing conspecific tree. For example, Montagnini et al. (1995) found that individual-tree stem biomass of

26-month-old *Jacaranda copaia* was about 40% greater when it was growing in mixed plantations than in monoculture. The greater growth resulted from less competition from non-jacaranda neighbours, and did not (yet?) result in any increased productivity at a stand level.

How might mixtures have higher productivity than monocultures? Net primary production could be greater in mixtures if one species could obtain more of a resource. For example, a shade-tolerant understorey species might take advantage of low-levels of light, water or nutrients that could not be used effectively by the overstorey species. How common are opportunities for capturing more resources in tropical plantations by using mixtures of species? In agroforestry situations, differences in rooting profiles between trees and annual crops may allow trees to tap water that would be inaccessible to crops (Vandermeer 1989). This may not be feasible in mixtures of tree species, where rooting profiles may be similar between species. Some tropical tree species are more tolerant of shade than others; the shade-tolerant component of a mixture also competes for other resources (such as water and nutrients), making the net effect on productivity uncertain.

Another way for mixtures to be more productive than monocultures would be if one species increased resource availability, such as through nitrogen-fixation (see Chapter 9). Under N-limiting conditions, a monoculture of the N-fixing species may be more productive than a monoculture of the non-N-fixing species, unless the non-N-fixer could use the N (or other resources) with a higher efficiency (NPP/unit resource) than the N-fixer. Binkley and Giardina (Chapter 9) present a case where N-fixing *Albizia falcataria* increased the N supply, but *Eucalyptus saligna* used the N more efficiently than the *Albizia*, leading to greater productivity in mixtures.

Aside from N-fixation, can any species increase nutrient supplies in soils? Given substantial differences in litterfall chemistry, and subsequent effects on soil microfauna and microflora, it may be possible for one species to increase soil nutrient supply relative to another species with poorer quality litter. However, this remains a largely unexplored subject for tropical plantations, and we know of no cases where differences in litter chemistry have led to opportunities for increased productivity of mixtures.

We note that the 'productivity' of a tropical plantation may be appropriately measured in terms other than NPP. The economic productivity of a plantation involves the balance between costs and product values. Mixtures might lead to greater economic productivity even if NPP is not increased if: damage by disease or insects is reduced; risk of plantation failure is reduced; the cost or value of products favours a mixture; or if the objectives of the landowner extend beyond simple wood production to include production of wildlife habitat, fodder or food crops (Vandermeer 1989). Any improvement of long-term soil fertility in mixtures could also justify use of mixed-species stands, but such expectations remain to be demonstrated. Plantation risks may be especially important, and mixtures may have different risks from pests and pathogens than monocultures. For example, Montagnini et al. (1995) found that mixed stands had a higher incidence of pest damage (number of plants with pest damage) than monocultures, but the severity of damage (number of damaged leaves or branches/tree) was lower in the mixture. The whole-rotation implications of pest damage in mixtures and monocultures require much more work before general insights will be available.

Nutritional Factors Controlling Stand Growth

Our discussion of stand growth patterns now turns to stand nutrition, because stand nutrition is easily affected by management activities, and sustaining stand nutrition is fundamental to sustaining productivity. How do the patterns of growth, carbon partitioning and nutrient uptake affect nutrient cycling and long-term productivity?

Nutrient supply

Under favourable environmental conditions, tropical plantations can use very large quantities of nutrients to achieve very high productivity. Most of the nutrients used in a current year are taken up from the soil in that year, but a substantial portion may come from internal stores that are replenished either through soil uptake or from resorption prior to tissue senescence (for a temperate forest review, see Nambiar and Fife 1991). Nitrogen-fixing trees may obtain more than half of their current requirement for N directly from the atmosphere.

Nutrients are taken up from the soil as simple ions, obtained either through microbial decomposition of organic matter (particularly for N and P), or from cation exchange sites (for cations such as Ca^{2+} and K^{+}). Several processes may replenish the soil pools, including recycling of plant litter, weathering of primary minerals, atmospheric deposition and fertilisation. Rates of nutrient uptake in fast-growing tropical plantations may exceed the rates of supply of nutrients, and rapid accumulation of nutrients in wood may deplete soil pools faster than they are replenished.

The uptake of nutrients may depend on both the soil nutrient supply and the surface area of roots and mycorrhizal fungi available for taking up ions. Absorbing area is particularly important for elements (such as P) which diffuse very poorly in soils. The uptake of P may differ between plantations, species or stand ages because of differences in soil P pools, or differences in production of fine roots and mycorrhizae.

Abundant evidence has shown that trees may alter soil nutrient supply, and that tree species may differ in their effects (reviewed by Sanchez et al. 1985; Binkley 1997b). Unfortunately, too few studies are available to provide general insights. Sanchez et al. (1985) describe a comparison of the effects of *Gmelina arborea* and *Pinus caribaea* on soil nutrients (to 1 m depth) in Brazil. Over 9 yr, *Gmelina* increased exchangeable Ca by 800 kg ha^{-1} and available P by 65 kg ha^{-1}, compared with only minor changes for *Pinus*. Available soil K was reduced by both species. Binkley (1997a) found that N-fixing *Albizia falcataria* increased the availability of soil N, but depleted available soil P relative to *Eucalyptus saligna*.

The total nutrient content present during growth of new tissues is usually calculated as the biomass of new tissues times the appropriate nutrient concentrations. The amount obtained from recycling from senescent foliage is often estimated as the nutrient quantity needed for production of new foliage, minus the nutrient content of senesced foliage. Nutrient uptake from the soil is then calculated as total requirement minus the recycled quantity. Caution is required, however, in interpreting nutrient content, calculated from data at a single point on the growth curve, in terms of nutrient requirement, especially for species that continue to grow throughout the year. Nutrient content data derived from sequential sampling of tree biomass would provide much better information on nutrient requirements.

The nutrient supply obtained from the soil may be estimated as the nutrient content of biomass increments (not production), plus the nutrient content of litterfall and fine root mortality. After the early stage of stand development, the nutrient content of litterfall is usually a larger portion of the annual nutrient use than the accumulation of nutrients in woody tissues. The quantity of nutrients used for root production has not been determined for many tropical plantations (see Chapter 8).

Nutrient accumulation and turnover

High rates of forest growth present a nutritional paradox: a high rate of nutrient supply leads to a high rate of biomass production, which entails 'locking up' a substantial amount of nutrients in tree biomass and thus may reduce nutrient availability in the soil. The rates of recycling of nutrients is fundamentally important to the sustained nutrition of a stand.

A large (and variable) portion of the nutrients taken up annually in a plantation are returned to the soil, where decomposition processes may recycle them into available pools. The partitioning of NPP to leaves, stems and roots differs among species and sites, and changes with stand development (as described earlier).

For nutrients such as nitrogen, accumulation into standing biomass is generally most rapid during the early stages of stand development when leaf area is expanding. Declining rates of nutrient accumulation in older stands may reflect either a reduced 'demand' after full leaf area is developed, or declining nutrient supplies in the soil; these alternative explanations remain largely unexamined. An example of the pattern of accumulation of N comes from a rapidly growing stand of *Eucalyptus grandis* from the cerrado of Brazil (Reis et al. 1987). Initially, greatest accumulation of N occurs in foliage. At about age 3 yr, the rate of wood accumulation increases as does accumulation of N in wood. These changes occur concurrently with a declining amount of N in leaves (Fig. 12.5). This species also accumulates large amounts of Ca, particularly in bark. Declines in foliar Ca with age were too small to allow increases in stem wood Ca; the lack of increase in stem wood Ca after age 3 yr may also indicate increasing Ca limitation or dilution of a rich pool that accumulated in earlier years.

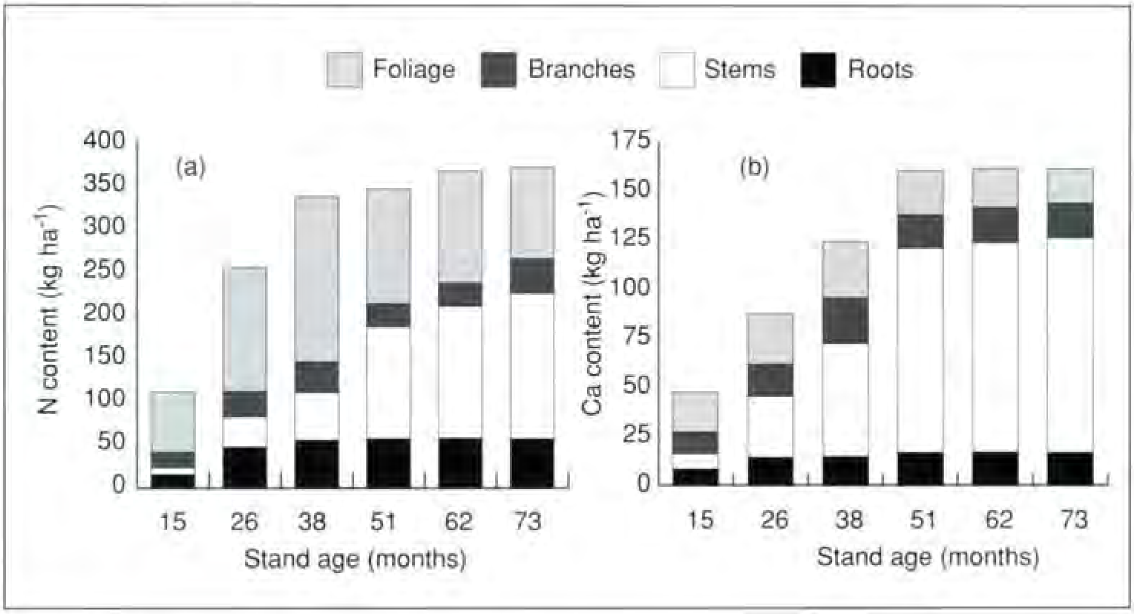

Figure 12.5 Nitrogen and calcium accumulation in biomass components for the good soil age sequence of *Eucalyptus grandis* in Figure 12.2. Nitrogen accumulation was concentrated in the foliage (especially early in stand development), whereas calcium accumulation was concentrated in the stems (data from Reis et al. 1985, 1987).

Differences in rates and amounts of nutrient accumulation among species may be large, even within a single genus. For example, five species of *Eucalyptus* were planted on a poor soil in Sao Paulo, Brazil. At age 10 yr, stem wood biomass ranged from 86 to 169 t ha^{-1}, with N contents ranging from 96 to 202 kg ha^{-1} (da Silva et al. 1983). *E. saligna* and *E. grandis* had the same biomass (about 160-170 t ha^{-1}), but *E. saligna* wood contained more than 50% more N and P than *E. grandis* wood. Another study (Wang et al. 1991) examined differences in biomass production and nutrient immobilisation in wood in replicated plantations of *E. robusta*, and nitrogen-fixing *Casuarina equisetifolia*, *Albizia procera* and *Leucaena leucocephala* in Puerto Rico. At age 5.5 yr, the *Casuarina* had the maximum biomass (199 t ha^{-1} total aboveground), followed by *Albizia* (124 t ha^{-1}), *Eucalyptus* (67 t ha^{-1}) and *Leucaena* (47 t ha^{-1}).

Litter from some plantation species decomposes slowly (e.g. *Eucalyptus* and *Pinus* spp. — Chapter 13) and the accumulated forest floor may become a significant repository of site nutrients. Some genera, such as *Eucalyptus*, *Pinus* and *Casuarina* appear to be very efficient in using nutrients to produce biomass (Bargali and Singh 1991; Wang et al. 1991; Binkley et al. 1992). However, the litter produced by these species may influence subsequent nutrient supply (Nandi et al. 1991; Richter et al. 1994; Wang et al. 1991). Plantation species that utilise nutrients efficiently typically produce plant litter with low nutrient contents and high carbon to nutrient ratios. Classically, residues of this type are expected to decompose more slowly, immobilise more nutrients during decomposition, and have slower rates of net nutrient mineralisation than nutrient-rich litter (Vitousek 1982). Such changes in these processes may buffer against nutrient loss from the site, but they could also reduce nutrient supply rates and increase the need for fertilisation. However, these expectations have rarely been examined experimentally, and experiments on the role of N availability as a control on decomposition have not always supported the classical expectations (Prescott 1995; Binkley 1997b). A great deal of experimental research is needed to develop general insights about the effect of litter quality on overall nutrient supply.

Given the lack of information from well-designed experiments, we surveyed the literature on rates of litter production and nutrient cycling in tree plantations ($n = 79$) and natural tropical forests ($n = 56$). We hoped to gain insights about patterns of nutrient cycling in litterfall and ecosystem productivity. The data for plantations come predominantly from Africa, South and Southeast Asia (mainly from the Indian sub-continent) with smaller data sets from northern Australia and the Americas. Across these studies, rates of litterfall and nutrient return depend very strongly on species, though we note that species selection may vary with site conditions (nutrient-demanding species may not be established on the poorest soils). Among the various species used in plantations, *Acacia auriculiformis, Albizia falcataria* and *Leucaena leucocephala* produced the greatest amounts of litter, with much lower rates for eucalypts, pines and poplars. The ranges of N and P content of litterfall overlapped between plantations and natural forests (Fig. 12.6), but a greater proportion of plantations have low nutrient contents of litterfall compared with natural forests. The plantations averaged about 25 to 50 kg N ha^{-1} yr^{-1} and 1 to 3 kg P ha^{-1} yr^{-1} in litterfall compared with 40 to 140 kg N ha^{-1} yr^{-1} and 3 to 8 kg P ha^{-1} yr^{-1} in natural forests. About 16% of the studies reported rates of N return less than 20 kg ha^{-1} yr^{-1}, whereas none of the natural forests showed such low rates. More than three-quarters of the plantations with low rates of N circulation were eucalypts or pines. Similarly about 19% of plantations cycled less P in litterfall than was observed for any natural forest and again most of these (more than 80%) were of eucalypt or pine species. Three factors could explain these differences:

- Plantations may have been established on less-fertile soils than natural forest sites in these studies;

- Species used in plantations (particularly eucalypts and pines) produce litter with lower nutrient concentrations;
- Differences in stand age obscure any comparison, as most plantations in the literature survey were younger than most natural forests.

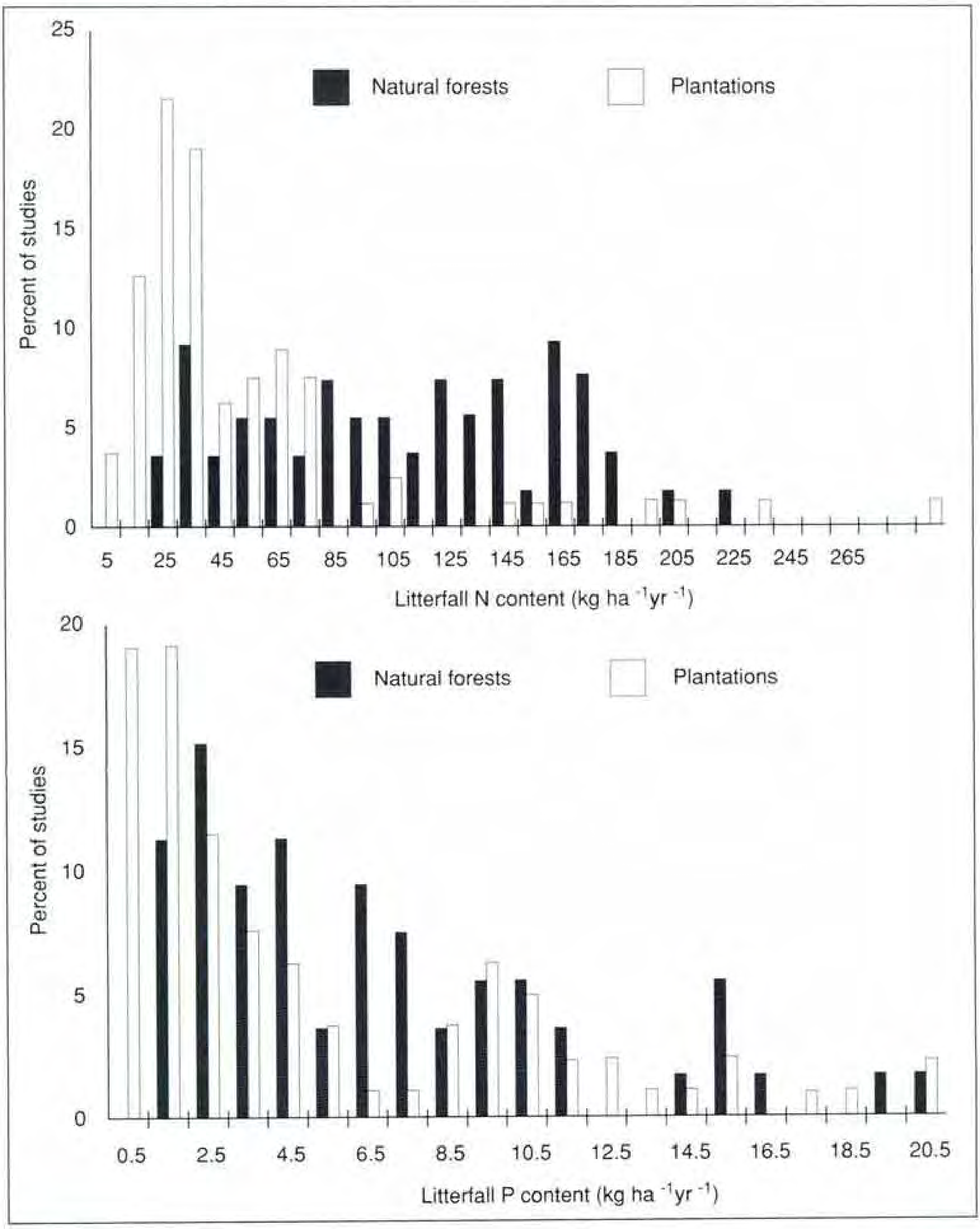

Figure 12.6 Histograms of N and P content of litterfall in tropical natural forests and plantations. A larger percentage of plantations show very low rates of nutrient flux in litterfall than do natural forests

The predominance of eucalypts and pines in the plantation studies suggests that the use of species with low rates of litterfall cycling of N and P probably accounts for the lower rates found for plantations. About one-quarter of the plantations, including stands of *Eucalyptus* and *Pinus* spp., *Tectona grandis* and *Populus deltoides*, produced litter with a lower ratio of N:P than was common for the natural forests (Fig. 12.7). The lower ratio of N:P might indicate that N limits growth of these plantations more frequently than the growth of natural forests, but this should be tested.

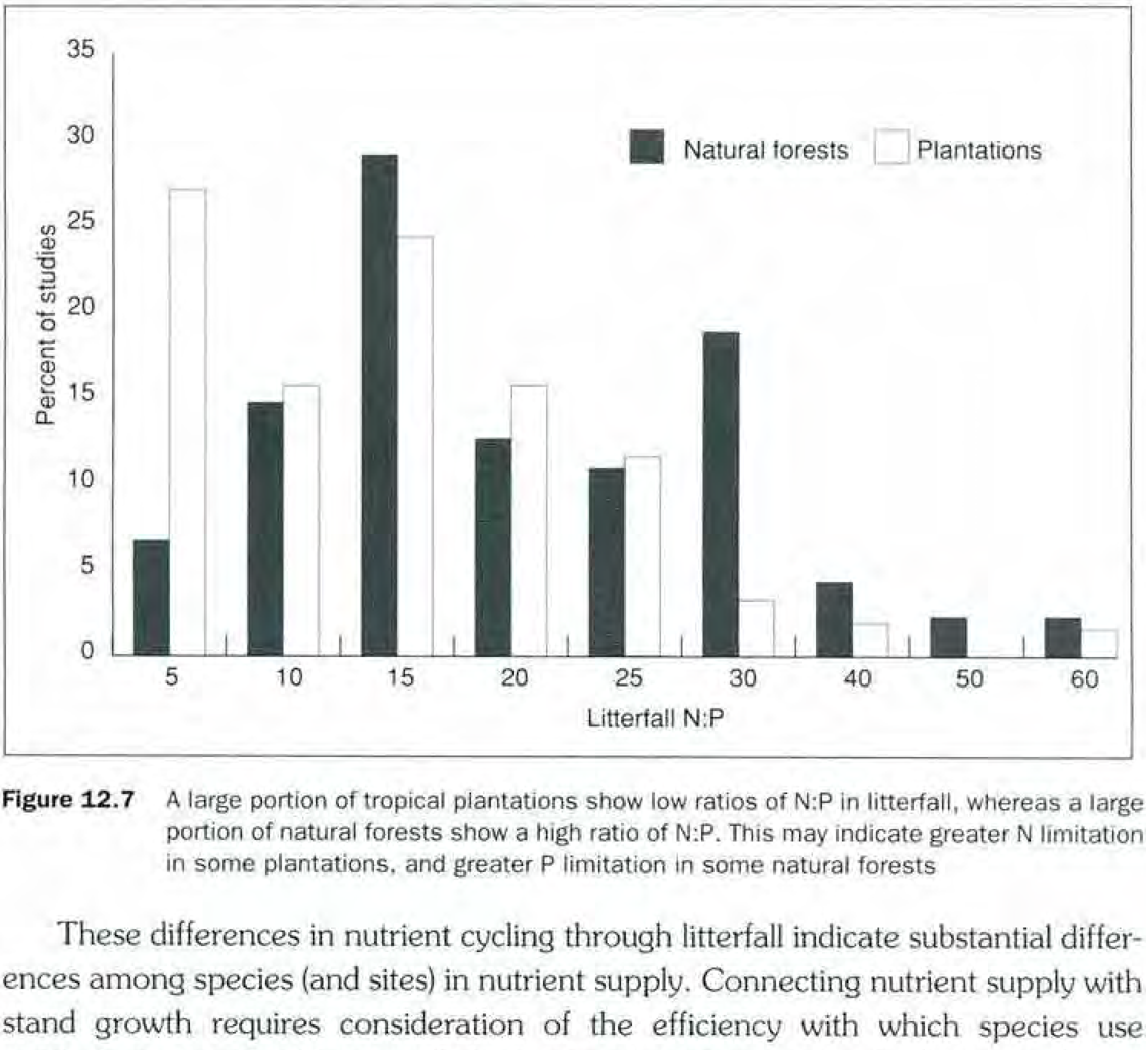

Figure 12.7 A large portion of tropical plantations show low ratios of N:P in litterfall, whereas a large portion of natural forests show a high ratio of N:P. This may indicate greater N limitation in some plantations, and greater P limitation in some natural forests

These differences in nutrient cycling through litterfall indicate substantial differences among species (and sites) in nutrient supply. Connecting nutrient supply with stand growth requires consideration of the efficiency with which species use nutrients to produce biomass. A high rate of nutrient uptake (and recycling) may lead to a high rate of production if a species is moderately or highly efficient at using nutrients; alternatively, a high rate of uptake coupled with low efficiency of use could lead to poor to moderate rates of production. For example, the *Albizia* plantations in Hawaii had higher rates of light interception and uptake of P than eucalypts (see Chapter 9), but the lower efficiency of using light and P by *Albizia* prevented any increase in productivity as a result of greater uptake.

Several definitions and methodologies to measure the efficiency of nutrient use of forest stands are common in the literature (Wang et al. 1991). Ideally, we would like to summarise the annual use of nutrients in tropical plantations in relation to stand productivity (i.e. ANPP per unit of nutrient taken up). Unfortunately, the annual use of nutrients has been estimated for very few tropical forests. Such information would be very valuable for matching rates of supply in soil with rates of uptake commensurate with expected rates of production.

Synthesis

High rates of production in tropical plantations result from high rates of supply of resources such as nutrients, water and light, and favourable environmental conditions for plant growth. The productivity of a given stand depends on these resource supplies, the efficiency of the trees in using these resources to produce biomass or stem wood, and any other factors such as pests, diseases and competition with non-crop plants. Productivity may be measured as total photosynthesis (GPP), the production of biomass after subtraction of plant respiration (NPP), the aboveground production (ANPP), stem wood production, or stem wood increment. These production rates can be expressed over a current period (as current annual increment), or averaged over a stand's lifetime (as mean annual increment).

Optimal management prescriptions need to account for these features. For example, the optimal rotation length for a plantation often depends on timing and magnitude of the post-peak decline in stand growth. If this decline in increment results from changes in stand nutrition, management activities that enhance or impair nutrition will change the optimal rotation length. Could fertilisation at age 6 yr extend the optimal rotation of a eucalypt plantation from age 7 to age 9 yr, reducing the number of hectares that incur regeneration costs each year? A great deal of research is needed to understand the opportunities for managing nutrition in relation to stand age and productivity.

The optimal species for a plantation also depends on management regimes; some species may yield a higher mean annual increment on a short rotation, whereas others would be superior in somewhat longer rotations. The responsiveness of species to nutrition management activities may also be very different, although little empirical information is available.

Are monocultures superior to mixed species stands? Current management regimes tend to prefer the simplicity and high productivity of monocultures. A variety of creative silvicultural opportunities may favour a more diverse approach to tropical plantations in the future. For example, one or two crops of agricultural crops could be included at the beginning of a rotation, substantially reducing the net cost of plantation establishment (cf. Couto et al. 1994, 1995). Mixtures of tree species could be advantageous in situations where the economic or ecological productivity of the mixture was greater than the monoculture, or where mixtures conferred other benefits such as reduced pest problems, improved wildlife habitat or increased understorey diversity of native plants.

High rates of production lead to high rates of nutrient accumulation in biomass. Based on the case studies presented here, a typical rotation-age plantation may contain 200 to more than 400 kg N ha^{-1}, and from 25 to 75 kg P ha^{-1}, with much of the variation resulting from species and rotation age. Harvesting removals represent large losses that may be unsustainable without large fertilisation inputs (see Chapters 10 and 11).

Key gaps in our understanding of stand-level growth and resource use centre on three topics:

1. What determines the timing of the growth peak early in stand development, and how flexible is the timing of the peak and the subsequent decline of annual growth? Declines in soil nutrient supplies (or fertiliser effects) account for at least part of the decline. Other factors may include balances between leaf area and woody biomass (per tree and per ha), changes in water relations with tree size, canopy abrasion from wind in tall trees, or changes in efficiency of light capture per unit of leaf area in older stands. Many management decisions, such as optimal economic rotations, may depend on the responsiveness of this growth pattern (in both timing of peak and magnitude of decline) to silvicultural treatments.
2. How do the supplies of resources change with stand development, and across rotations? Nutrient supply may change as a result of fertilisation, nutrient accumulation in biomass and site preparation activities between rotations, and with changes in recycling rates because of differences in litter chemistry and soil communities. Water supplies may change as changes in leaf area lead to changes in interception loss, or as trees draw down the water supply stored deep in soils. The effects of increasing supplies of atmospheric CO_2 may also be critical to the future of tropical plantations.
3. Long-term trials (2 or more rotations) need to be established, with direct measurements of the processes that control plantation growth. Many studies have documented patterns in tree growth, but few provide much insight about what controlled the pattern in growth, or how flexible the pattern might be. The growth patterns from hundreds of stands of *Gmelina arborea* in Brazil (Fig. 12.1) documented a common growth pattern, but give us no insights about why current growth declined before the stands were even 4 yr old. At a minimum, such studies should estimate dynamics in stand leaf area (Chapter 6) (or perhaps just light interception?) and changes in nutrient supplies in the soil.

Acknowledgments

We thank the co-authors of this book for providing insights, ideas and examples for this chapter, particularly Walter de Lima, Leonardo Gonçalves, Florencia Montagnini and Henry Gholz. Mike Ryan's insights were especially helpful regarding changes in growth and respiration with stand age. We thank Tom Schubert, formerly of BioEnergy Development Corporation, for productivity data for the *Eucalyptus* trials in Hawaii. Writing of this chapter was supported in part by National Science Foundation Grant DEB93-06356, and by McIntire-Stennis appropriations to Colorado State University.

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13

Organic Matter Accretion, Decomposition and Mineralisation

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Abstract

In natural and plantation forests, biogeochemical nutrient cycling is dominated by litter production and decomposition. In this chapter we focus on litter accumulation and decomposition and compare and contrast the nutrient cycling processes occurring in plantations with those of the natural forests. We review the current status of knowledge on the impact of plantations on soil nutrient status, suggest management options to ameliorate fertility decline in intensively-managed plantations and identify areas where further research is necessary. Species of *Eucalyptus* and *Pinus*, which make up about one quarter of the total area of tropical plantations, generally have higher nutrient-use efficiencies (carbon gain per unit of nutrient taken up), and produce litter that is poorer in nutrients than most native tropical trees and other common plantation species. Litter in plantations of *Eucalyptus* and *Pinus*, and other genera such as *Casuarina*, usually decays more slowly and accumulates on the forest floor to a greater extent than plant detritus in native tropical forests. The distribution of carbon within ecosystem compartments and its effect on rates of nutrient cycling appears to be a fundamental difference between these species and many native tropical forests. Tree legumes produce litter that is richer in nutrients than *Eucalyptus* and *Pinus* species. However, even in these plantations, some species (e.g. *Acacia auriculiformis*) produce litter which is slow to decay and which accumulates in substantial amounts on the forest floor. The limited studies available suggest that rate of nutrient release during decomposition of tropical plant litter may be controlled by factors similar to those found to be important in temperate forests. Plantation species have been found to affect soil chemical properties and in some cases to reduce the stores and flux rates of available plant nutrients in soil. The extent of changes in soil fertility depends on initial soil conditions, on the tree species and on management practices used during the rotations and at harvest. On high quality sites, several rotations of tree crops may result in little deterioration in soil properties. On poor sites, common in the tropics, reductions in soil nutrient status and stand productivity are likely to occur unless nutrient supplies are enriched with fertilizers. Mixed species plantings, especially utilising N-fixing trees and shrubs, and management practices which maintain high-nutrient plant residues on the site within and between rotations are options for improving plantation forestry.

THE PRIMARY factors controlling forest productivity are energy, water and nutrient supply. In natural forests, nutrient requirements for growth and maintenance are met through nutrient cycling. Switzer and Nelson (1972) identified three processes of nutrient cycling, namely: i) geochemical cycling in which nutrients are supplied from weathering of soil minerals and through input from the atmosphere or are lost in volatile forms or through drainage; ii) biochemical cycling where nutrients are redistributed within the plant to meet demands for growth; and iii) biogeochemical cycling in which nutrients released from plant residues or through canopy leaching or stemflow enter the soil and then are taken up by the plant roots. Each of these processes can be affected when current land use is replaced by short-rotation tree cropping. In most natural forests and plantations, biogeochemical nutrient cycling is dominated by litter production and decomposition. Litter from both above- and belowground sources is important in these processes. However, for most forests, and for tropical plantations in particular, most information available on biogeochemical nutrient cycling is confined to the aboveground detritus. In this review we therefore focus primarily on this pathway. This does not imply a lack of importance of belowground litter production but rather reflects the difficulties attached to studies of root production and turnover and the paucity of data available on these processes (see Chapter 8).

Plant residues accumulating on the forest floor disappear by various processes. Soil fauna consume and fragment the litter and incorporate it in the surface layers of the soil. Water-soluble compounds are leached from the residues and carbon is mineralised and respired as CO_2 through the action of microorganisms. The importance of each process depends on the nature of the plant residues, on the micro-environment at the soil surface and on the qualitative and quantitative composition of the decomposer organisms (Swift et al. 1979). During litter breakdown, release of plant nutrients occurs principally through microbially-mediated biochemical reactions. Mineralised nutrients are available for uptake and reuse by the plant community. Nutrients may also be immobilised in the microbial biomass or by reactions with soil minerals or be lost from the ecosystem through leaching or in volatile forms.

For evaluating the functional aspects of nutrient cycling in tropical plantations and to predict the impact of plantations on the soil environment, it is common to compare the attributes of plantations with adjacent native forests. This is best done by evaluating the effect of changing land management at the same site over time. An alternative is to compare at one time adjacent or similar plantation and natural forest sites (Sanchez et al. 1985). Only a few studies of the first type are available (Nandi et al. 1991; Richter et al. 1994). Most studies are of the second type. This may account in part for the conflicting views of the impact of short-rotation plantations on soil fertility and the differing assessments of their long-term sustainability. Nevertheless, there is now an increasing amount of information on nutrient cycling in tropical plantations which allows some generalisations to be made of their impact on the soil environment.

Many native tropical forests grow on sites with highly weathered soils having low nutrient status. The fact that these forests can attain such stature has been attributed in part to mechanisms they have evolved to acquire and conserve nutrients (Golley 1983a). In mature undisturbed forests, most NPP is discarded as litterfall. Nutrient requirements are largely met by decomposition and mineralisation of these residues. In many short-rotation plantations (e.g. 8–10 yr pulpwood production) much of annual NPP is directed towards growth of the living biomass, especially the developing tree canopy, and nutrient cycling is dominated by uptake and accumulation in the tree. During the early stage of tree growth the litter cycle is not well developed and stand nutrient requirements are derived largely from soil reserves. At harvest a major proportion of some accumulated nutrients, especially nitrogen and phosphorus, is contained in foliage, twig and small branch material. Research has shown that in areas of high rainfall where native tropical forests are cleared and replaced by other land uses, immediate and severe losses of plant nutrients and soil organic matter are likely (Nye and Greenland 1964; Herrera and Jordan 1981; Tiessen et al. 1994). Similar processes can occur when successive rotations of plantations are harvested. Silvicultural practices which retain and protect litter and harvest residues following logging will be critical for sustainability of tropical plantations.

Tropical plantations cover approximately 43 million ha (Chapter 1). They are dominated by *Eucalyptus* and *Pinus* species which together account for about one quarter of the area of tropical plantations. Other species such as *Albizia falcataria, Acacia auriculiformis, Acacia mangium, Gmelina arborea* and *Casuarina equisetifolia* occupy comparatively smaller areas. In terms of nutrient cycling, the concentration of research on eucalypts and pines is important, because species of these genera often have higher nutrient-use efficiencies (NPP per unit of nutrient uptake—Bargali and Singh 1991; Binkley et al. 1992) and litter that is poorer in nutrients (Lugo et al. 1990b; Wang et al. 1991) than other plantation species and natural tropical forests. These two factors can markedly affect biogeochemical nutrient cycling processes such as rates of residue decomposition and accumulation, nutrient mineralisation from litter and soil organic matter and plant nutrient uptake from soil.

In this chapter we focus on decomposition and biogeochemical nutrient cycling and compare and contrast the functional processes occurring in plantations with those of the natural forests. We review current knowledge on the impact of intensively-managed plantations on soil nutrient status and suggest management options for maintaining site fertility. Finally we identify gaps in knowledge and suggest some topics for research necessary to provide information critical in quantitatively assessing sustainability of short-rotation plantations.

Litter Accumulation

Litter accumulation in tropical forests and plantations and temperate forests

Amounts of litter accumulated under natural tropical forests, especially in tropical moist forests, are often small due to high decomposition rates (Olson 1963). Although Rodin and Brazilevich (1967) originally suggested a general rule relating accumulation on the forest floor to increasing distance from the tropics, it is now recognised that this relationship is often masked by variability within forests of each climatic zone (Vogt et al. 1986). An example of such variation is the large accumulation of litter (120 t ha^{-1}) under plantations of *Casuarina equisetifolia* used in afforestation of the coastal dune systems of Senegal (Mailly and Margolis 1992). Similar amounts are found in many boreal ecosystems. In moist tropical forests, accumulation of forest floor mass is usually much less and for many ecosystems amounts to only 2 to 11 t ha^{-1} (Proctor 1987).

The variation in mass of forest floor litter between different tropical plantations reflects the predominant influence of species characteristics, stand age, growth rates, climatic conditions and soil properties. Litter accumulation across a broad range of species, stand age and locality generally falls within the range <1.0 to 22 t ha^{-1} (Table 13.1). Rates of forest floor accumulation in plantation forests can differ markedly between species planted on the same site. In general, species of eucalypt, pine and casuarina accumulate more litter compared to many other plantation species. Large accumulations under eucalypt plantations have been found in several countries, e.g. in Australia (Bradstock 1981), the Congo region (Bernhard-Reversat 1993) and India (Singh et al. 1993; Toky and Singh 1993) and is probably due in part to the sclerophyllous nature of eucalypt leaves which break down relatively slowly. Likewise, forest floor development under various species of pines exceeds that of the other common plantation species in many regions at lower latitudes, e.g. in North Louisiana, USA (Lockaby and Taylor-Boyd 1986), Indonesia (Gunadi 1994), Nigeria (Kadeba and Aduayi 1985) and Puerto Rico (Cuevas et al. (1991). *Casuarina equisetifolia* (Sugur 1989; Lugo et al. 1990a; Mailly and Margolis 1992), *Acacia auriculiformis* (Swamy 1989; Sankaran et al. 1993) and *Rhizophora mucronata* (mangrove—Sukardjo and Yamada 1992) are other plantation species which accumulate large amounts of forest floor litter.

There are limited data on litter accumulation in native tropical forests (Table 13.2). On a regional basis, accumulations in African forests range from 1.7 t ha^{-1} in a moist deciduous forest in Nigeria (Hopkins 1966) to 13.3 t ha^{-1} in an evergreen forest in Gabon (Hladik 1978). In the South American region, the forest floor mass in native tropical forests ranges from 3.1 to 16.5 t ha^{-1}, the highest value being for a lower montane forest in Colombia. Montane forests usually accumulate more litter than other native forests in the tropics (Jenny et al. 1949; Tanner 1980) probably because of low nutrient content of litterfall and climatic factors which result in slow decomposition. Litter accumulation in tropical forests in India ranges from 4.1 to 6.5 t ha^{-1} in evergreen, moist deciduous and shola forests in Karnataka. An exceptional value of 21.1 t ha^{-1} was recorded in a moist deciduous forest in Karnataka (Bhat 1990). In Sarawak, a series of contrasting lowland rainforests including alluvial, dipterocarp, heath forest and forest over limestone accumulated between 5.5 t and 7.1 t ha^{-1} litter (Anderson et al. 1983) while a lower dipterocarp forest in Malaysia accumulated 3.2 t ha^{-1} (Ogawa 1978). In Australian rainforest, litter accumulation varies between 4.4 to 6.3 t ha^{-1} (Spain 1984). Thus the litter standing crop in tropical forests ranges from a low value of 1.7 up to 21.1 t ha^{-1}. However, more than 75% of the values for litter accumulation in the native tropical forests considered in this review fell below 7 t ha^{-1} and the mean accumulation was 6 t ha^{-1}.

Litter accumulation in temperate forests varies widely (Vogt et al. 1986). On a regional basis (Table 13.3), temperate eucalypt forests in Australia accumulate smaller amounts of litter (range 12 to 22 t ha^{-1}) than many other species in warm temperate, cold temperate and boreal forests. In part this may be due to combustion of litter by fires which periodically burn many eucalypt forests in Australia (Raison et al. 1983). Data on litter accumulation in a range of other forests in the temperate region vary from 2.1 t in a oak hornbeam forest in Poland (De Angelis et al. 1981) to 117 t ha^{-1} in a balsam fir forest in New England, USA (Vogt et al. 1986). About 60% of the values in our data set fell within the range 10 to 30 t ha^{-1}. However, a number of temperate forests accumulated much larger amounts of litter, notably a Scots pine forest in Switzerland (110 t ha^{-1}), a spruce forest in Germany (110 t ha^{-1}), and a ponderosa pine forest (113 t ha^{-1}) and a balsam fir forest (117 t ha^{-1}) in USA. For all temperate forests in our data set mean forest floor accumulation was 41 t ha^{-1}. These data indicate that temperate forests generally accumulate greater amounts of litter than natural tropical forests and tropical plantations (Bray and Gorham 1964; Vogt et al. 1986).

Table 13.1 Mean litter accumulation and litter decay rates in tropical plantations grouped by species, together with the number of observations in each forest type and the range of each parameter

Species	Age range(yr)	Location	Litter accumulation (t ha^{-1})			Age range(yr)	Location	Decay constant k (yr^{-1})		
			No.	Mean	Range			No.	Mean	Range
Eucalyptus spp.	2–27	India, Congo, Puerto Rico, New South Wales (Australia)	15	8.2	0.8–21.6	2–40	Congo, Ethiopia, New South Wales (Australia), India	19	0.90	0.38–1.50
Pinus spp.	7–31	Nigeria, Puerto Rico, Indonesia, North Louisiana (USA), India	5	14.5	10.5–21.0	7–57	Puerto Rico, North Louisiana (USA), India	7	0.88	0.38–1.50
Tectona grandis	15–56	India	3	7.7	5.5–12.1	25–57	India	5	1.62	1.21–2.00
Acacia spp.	4–11	India, Malaysia, Congo	6	7.7	3.0–14.8	4–11	India, Malaysia, Congo	9	1.04	0.72–1.40
Populus deltoides	4	India	1	4.6	–	4	India	1	1.05	–
Leucaena leucocephala	4–8	Puerto Rico, India	4	8.1	6.5–12.3	2–8	India	3	0.62	0.11–0.89
Shorea robusta	–	–	–	–	–	30–57	India	3	1.51	0.88–1.97
Casuarina equisetifolia	6–34	Puerto Rico, India, Senegal	3	40.8	3.1–120.3	–	–	–	–	–
Albizia spp.	5.5	Puerto Rico	1	10.2	–	10	India	1	1.67	–
Dalbergia sissoo	–	–	–	–	–	17	India	1	1.32	–
Bombax ceiba	–	–	–	–	–	20	India	1	1.67	–

Table 13.2 Mean litter accumulation and litter decay rates in natural tropical forests grouped by forest type, together with the number of observations in each forest type and the range of each parameter

Forest type	Location	Litter accumulation (t ha^{-1})			Location	Decay constant *k* (yr^{-1})		
		No.	Mean	Range		No.	Mean	Range
Evergreen to semi-evergreen	Brazil, Nigeria, Puerto Rico, Trinidad, India	12	3.5	3.0–5.2	Brazil, Ethiopia, India, Puerto Rico, Trinidad, Zaire	20	2.2	0.6–3.9
Moist deciduous to semi-deciduous	Ghana,Nigeria, India	4	4.8	1.7–6.5	Ghana, India	9	3.6	1.9–5.3
Dry deciduous to semi-deciduous	India	1	0.6	–	Thailand, India	3	1.4	0.5–2.8
Mixed forests	Nigeria, Colombia, India	5	10.1	5.0–21.1	Nigeria, Colombia, India	5	1.0	0.3–1.7
Montane forests	Colombia, Jamaica, New Guinea	4	11.0	6.5–16.5	Jamaica, New Guinea	3	0.9	0.5–1.2
Australian rainforests (mixed)	Australia	3	5.3	4.4–6.3	Australia	7	1.3	0.6–2.2
Eucalypt forests	Australia	–	–	–	Australia	1	0.4	
Dipterocarp forests	Malaysia	3	4.7	3.2–5.9	Malaysia	2	2.5	1.7–3.3
Lowland rainforests	Malaysia, Mexico	5	5.8	5.5–7.1	Malaysia	5	2.6	1.4–5.1
Shola forests	India	2	3.9	2.9–4.9	India	1	2.9	–

Montane, eucalypt and shola forests are evergreen types. However, because they differ widely in many respects from other tropical evergreen forests they are grouped separately.

Table 13.3 Mean litter acumulation and litter decay rates in selected natural temperate and boreal forests grouped by forest type and geographic region, together with the number of observations in each forest type and the range of each parameter

Forest type	Location	Litter accumulation (t ha^{-1})			Decay constant k (yr^{-1})		
		No.	Mean	Range	No.	Mean	Range
Eucalypt forests (broad leaved evergreen)	Australia	11	16.6	12.2–22.2	14	0.42	0.19–0.68
Nothofagus forest (broad leaved evergreen)	Australia	1	8.1	–	–	–	–
Needle-leaved evergreen (temperate)	Canada	2	61.2	20.3–102.0	2	0.34	0.30–0.36
Needle-leaved evergreen (boreal)	Canada	2	76.0	65.0–87.0	–	–	–
Broad-leaved deciduous	Canada	1	60.0	–	2	0.30	0.11–0.49
Needle-leaved evergreen (temperate)	England, Finland, Scotland, Ireland, Netherlands	12	48.0	18.9–111.0	1	0.65	–
Broad-leaved deciduous	England, Finland, Netherlands, Poland, Germany	8	19.8	2.1–39.0	–	–	–
Needle-leaved evergreen (boreal)	Germany	3	70.7	49.0–111.0	–	–	–
Needle-leaved evergreen (temperate)	Japan	2	38.8	26.8–50.8	–	–	–
Needle-leaved evergreen (temperate)	USA	22	33.8	0.7–117.0	1	0.46	–
Broad-leaved deciduous	USA	8	36.5	6.0–59.6	2	0.28	0.08–0.47
Needle-leaved evergreen (temperate)	USSR	18	26.5	17.4–61.0	–	–	–

Comparison of litter accumulation in natural tropical forests and plantations

It has been estimated that natural forests accumulate leaf litter which is equivalent to 2% of their aboveground biomass (Brown and Lugo 1982). This proportion is often greater in plantations. For example, in Puerto Rico, Lugo et al. (1990a) reported that *Casuarina* and *Albizia* plantations accumulated leaf litter that was equivalent to 10% of aboveground biomass, with higher rates for eucalypt and *Leucaena* plantations. Likewise accumulated litter usually represents a smaller proportion of annual litterfall in native tropical forests than in plantations. Thus the standing crop of litter in natural forests in Karnataka, India, was equivalent to 31% to 51% of the annual litterfall (Swamy 1989). In adjacent plantations of teak, *Acacia auriculiformis* and *Eucalyptus tereticornis* the equivalent proportions were 48%, 85% and 90% respectively. The total amount of accumulated litter is also often greater in plantations than in natural tropical forests. In Puerto Rico, Cuevas et al. (1991) found that an 11-yr-old *Pinus caribaea* plantation accumulated twice as much litter as a paired broad-leaf secondary forest. When plantations of *Eucalyptus grandis* replaced naturally occurring subtropical rainforest in eastern Australia, litter accumulation increased 1.5 fold (Turner and Lambert 1983, 1989). Similarly, where conifers have been used as plantation species in the tropics, the amount of accumulated forest floor litter often exceeds that found in adjacent native forests (Hopkins 1966; Cornforth 1970; Kadeba and Aduayi 1985). Brown and Lugo (1982) identified the greater amount of accumulated litter and the greater proportion of litter relative to aboveground biomass in plantations as compared with natural forest as a fundamental difference between these forest types in the tropics.

The amount of accumulated forest floor litter is determined by the balance between the rate of litterfall accession and the rate of litter decomposition. Accumulation on the forest floor in some tropical plantations at a rate higher than found in native forests appears to be due to maintenance of annual litterfall accessions and to the lower rates of decomposition of plantation litter. Slow decay can result from a number of factors, including: i) low nutrient status of the litter; ii) low nutrient status of the soil; iii) unfavourable environmental conditions for decomposition (e.g. moisture deficit in soil and litter, very high or very low temperature, adverse soil pH); iv) physicochemical properties of the litter such leaf toughness, polyphenol and tannin content; or v) a low density and diversity of the decomposer population. Where species such as eucalypts or pines replace the native species, the rate of litterfall input can be similar to that in native species while decomposition is slower for one or more of the above reasons, leading to greater accumulation of forest floor litter. Lugo et al. (1990a) suggested that this characteristic difference between natural and plantation forests in the tropics may be important in moderating erosion following harvesting and that accumulated nutrients in the litter layer of plantations may be critical for supporting growth in the next rotation.

Nutrients in the forest floor

Rates of nutrient accumulation in the forest floor of tropical plantations (Table 13.4) depend on both the climate of the region and the species used in the plantation. For example, where plantations include nitrogen-fixing species, accumulation of N in the forest floor can be substantial. This is especially so where climatic conditions do not favour rapid litter decomposition. For example, *Casuarina equisetifolia* plantations in Senegal accumulated nitrogen in litter at a rate of 45 kg $ha^{-1}yr^{-1}$ and in stands 34 yr old almost 1600 kg ha^{-1} was retained in surface litter. This, together with accumulation in surface mineral soil, corresponded to accretion of nitrogen to the ecosystem through fixation by the actinorhizal root symbioses exceeding 75 kg ha^{-1} yr^{-1} (Mailly and Margolis 1992). Under moister conditions in Puerto Rico, *Casuarina* also accumulated nitrogen rapidly and after 5.5 yr more than 250 kg ha^{-1} was retained in litter (Wang et al. 1991). Large buildup of forest floor nitrogen appears to be a characteristic of *Casuarina*, probably due to accretion through N-fixation and the relatively slow decomposition of the litter. *Leucaena leucocephala* also accumulates large amounts of N, one 8-yr-old stand in Hisar, India, having almost 300 kg N ha^{-1} in the litter layer (Toky and Singh 1993).

Other plantation species also accumulate substantial amounts of nutrients in litter where decomposition is slow or nutrient immobilisation occurs. For example, in 26-yr-old plantations in Puerto Rico, *Pinus caribaea* and *P. elliottii* had accumulated 143 kg N ha^{-1}, 9 kg P ha^{-1} and 44 kg K ha^{-1} in the litter layer. *Eucalyptus patentinervis* had less N and P but more Ca and Mg than expected from litter accumulation rates (Lugo et al. 1990b). Other studies have also reported large accumulations of nutrients under eucalypt plantations (Negi et al. 1988) and significant increases in litter nutrients with increasing age of the stands, indicating that accession rates exceeded rates of turnover in the forest floor (Toky and Singh 1993). For some species the distribution of nutrients in litter does not always correlate with rate of forest floor accumulation, indicating that microbial immobilisation can be an important factor affecting nutrient accumulation. For example, *Swietenia* plantations had comparatively low standing crops of litter but accumulated 137 kg N ha^{-1} in the forest floor (Lugo et al. 1990b).

Examples of nutrient accumulation in the forest floor of natural tropical forests are given in Table 13.5. The nutrient content of the standing crop of litter in natural tropical forests ranged from 7 to 96 kg ha^{-1} for N, 0.2 to 5 for P, 1 to 16 for K, 4 to 270 for Ca and 0.7 to 14 for Mg, with mean accumulations of 52, 2.4, 5, 61 and 7 for N, P, K, Ca and Mg respectively. These data indicate that when considering the mean across all species and forest types, plantations in the tropics accumulate a greater amount of N, P, K, Ca and Mg in the litter layer than natural forests. However, within each forest group there is a large variation in the amount of nutrients stored in the forest floor. Slow decay of litter and the resultant immobilisation of nutrients are the main causes of the large nutrient accumulations in the floor of some plantations. This slow turnover in accumulating forest litter could induce nutrient-based limitation of tree growth as the plantations age. Nutrients stored in litter at time of harvest can be a valuable resource for long-term productivity, but methods of site preparation for replanting may be critical in minimising their loss.

Litter Decomposition

Factors controlling decomposition

Decomposition plays a critical role in stand nutrition through its contribution to nutrient cycling and formation of soil organic matter. The primary factors affecting rate at which litter decomposes are the composition of the decomposer organisms, the physical environment (principally the microclimate of the forest floor) and the quality of the accumulated resource of plant residues (Swift et al. 1979). These factors together determine the residence time of plant detritus and also the rate of nutrient cycling. As decomposition proceeds, part of the carbon content of the residue is respired as CO_2 and some may be leached from the soil. Secondary products of decomposition form the source material for soil organic matter. Following decomposition of surface litter, remaining organic compounds may be incorporated in humus and contribute to the exchange complex of the soil. The rate at which nutrients are released during decomposition can differ markedly between different elements and is influenced by physical and biochemical characteristics of the residues and the heterotrophic demand of the decomposer organisms. As discussed earlier, replacement of natural vegetation with plantations of either native or introduced species can affect litter decomposition and consequently modify soil organic matter formation and the rate of biogeochemical nutrient cycling.

The global trend in turnover of soil organic matter, as indicated by respiratory output, shows that decomposition is inversely related to latitude (Schlesinger 1977), although there are exceptions to this general trend (Anderson et al. 1983; Sukardjo and Yamada 1992). Data from a broad range of sites also indicate that there is some degree of overlap between rates of decomposition in some natural tropical and temperate forests (Anderson and Swift 1983). The probable reason for this is that the rapidity of decay of plant residues is not determined by one single factor, but rather by the interplay of climate, resource quality and the decomposer community.

Litter may quickly build up beneath plantations in the humid tropics, as is illustrated in the 6-yr-old stand of *Acacia mangium* shown left and in detail below. The litter and the mineral soil remain clearly separated, but the interface has a remarkable concentration of fine roots and fungal mycelia. This colonisation may be evident in the second year of the plantation, and is an important mechanism for nutrient conservation.
(Photos: E.K.S. Nambiar)

Table 13.4 Accumulated nitrogen, phosphorus, potassium, calcium and magnesium in the litter layer of selected tropical plantations grouped by species, together with the number of observations in each forest type and the range of each parameter

Plantation species	Age (yr)	Location	N (kg ha^{-1})			P (kg ha^{-1})			K (kg ha^{-1})			Ca (kg ha^{-1})			Mg (kg ha^{-1})		
			No.	Mean	Range	No.	Mean	Range	No.	Mean	Range	No.	Mean	Range	No.	Mean	Range
Eucalyptus spp.	4–75	Australia, India, Puerto Rico	10	81.6	22.0–222.5	10	5.5	2.0–18.7	10	18.6	4.0–34.6	10	91.0	18.0–206.6	10	16.3	1.0–42.3
Pinus spp.	7–26	Nigeria, Puerto Rico, India, North Louisiana (USA)	7	154.9	59.9–276.9	7	18.5	2.3–38.3	7	36.4	3.5–55.4	7	82.2	66.6–113.7	7	29.4	4.1–40.7
Leucaena leucocephala	4–8	India	2	222.7	147.5–297.9	2	17.7	11.6–23.7	2	40.3	25.1–55.4	2	80.7	57.0–104.4	2	12.2	7.8–16.6
Acacia nilotica	4–8	India	2	96.8	85.0–108.6	2	5.7	4.8–6.5	2	14.1	11.4–16.8	2	31.6	27.2–35.9	2	5.9	5.0–6.7
Casuarina equisetifolia	6–34	Senegal	4	661.2	245.0–1567.0	4	4.1	1.7–9.5	4	11.4	5.5–12.9	4	120.5	56.0–276.0	4	31.6	13.1–63.8

Table 13.5 Accumulated nitrogen, phosphorus, potassium, calcium and magnesium in the litter layer of natural tropical forests

No.	Species	Geographic region	Nutrients accumulated (kg ha⁻¹)					Reference
			N	P	K	Ca	Mg	
1	Secondary rainforest	Nigeria	67.0	4.0	16.0	97.0	14.0[a]	Swift et al. 1981
2	Lowland evergreen rainforest	Maraca Island, Brazil	49.2	2.4	8.2	32.0	8.1	Scott et al. 1992
3	*Mora excelsa* forest	Trinidad	48.0	3.0	3.0	19.0	7.0[a]	Cornforth 1970
4	*M. excelsa* forest	Trinidad	35.0	2.0	2.0	15.0	6.0	Cornforth 1970
5	*Shorea robusta* stand	Uttar Pradesh, India	7.0	0.2	2.0	4.0	6.0[b]	Singh et al. 1993
6	Alluvial forest	National Park, Sarawak	39.0	1.9	4.4	110.0	4.7	Anderson et al. 1983
7	Dipterocarp forest	National Park, Sarawak	42.0	1.0	9.6	7.2	3.8	Anderson et al. 1983
8	Heath forest	National Park, Sarawak	26.0	0.9	4.8	44.0	4.5	Anderson et al. 1983
9	Forest over limestone	National Park, Sarawak	78.0	2.6	4.7	270.0	14.0	Anderson et al. 1983
10	*Eucalyptus* forest	Queensland, Australia	194.9 46.2	6.8 1.5	22.6 2.8	141.8 28.6	34.0[c] 3.2[a]	Rogers and Westman 1977
11	Lower montane forest	New Guinea	91.0	4.8	11.5	96.0	14.5	Edwards 1982
12	Moist semi-deciduous forest	New Guinea	96.0	4.0	1.2	10.4	0.7	Enright 1979

[a] Leaf litter only; [b] Nutrients remaining after one yr; [c] Leaf, bark and wood litter (wood size unspecified)

Climatic effects can have a marked impact on decomposition rates and the patterns of mineralisation resulting from biogeochemical nutrient cycling (Swift et al. 1979; Cornejo et al. 1994). In tropical forests, environmental conditions usually favour rapid decomposition of litter compared to temperate and boreal forests because temperatures are favourable for decomposer activity year round (Olson 1963; Jordan 1985; Chapter 3). Where rainfall is seasonal, moisture becomes an important regulator of litterfall and decomposition. This in turn can result in marked pulses in amounts of nutrient available for plant uptake (Lodge 1987; Lodge et al. 1994). This phenomenon commonly occurs in seasonally-dry tropical forests and is due to the interaction of factors affecting rates of litter accession and decomposition, and nutrient mineralisation. In these forests, during periods of water stress, the rate of litterfall may be high and decomposition slow. The onset of the wet season accelerates decomposition and releases available nutrients (Swift et al 1981). Furthermore, wetting and drying cycles can accelerate the mineralisation of labile nutrients such as those stored in microbial biomass, and also increase the rate of turnover of more recalcitrant and protected organic pools of litter and surface soil (Van Veen et al. 1984; Cabrera 1993).

Rapid organic matter decomposition in tropical forests is mediated by the generally high bacterial cell counts and fungal hyphal lengths in their soils compared to those in temperate and boreal forests (Swift et al. 1979). In the tropics, favourable environmental conditions, especially soil temperature, also enhance rates of microbial turnover leading to rapid catabolism and nutrient mineralisation. Tropical forests generally contain a more diverse soil fauna than do temperate and subalpine forests, but they often have smaller numbers and biomass of meso- and macrofauna (Swift et al. 1979), probably because of the lack of a substantial litter layer in many tropical forests (Golley 1983b). Within the tropics, the amount and type of accumulated litter can affect composition of litter and soil fauna (Plowman 1979). The functional characteristics of soil fauna such as earthworms also differ markedly between global regions (Anderson and Swift 1983) probably because of differences in the nature of litter and soil organic matter (Jordan 1985). There is some evidence (Anderson and Swift 1983; Anderson et al. 1983) of regional differences within the tropics in decay rates, with more rapid decomposition occurring in West African forests than in the Americas or Southeast Asia. Removal of native vegetation can reduce soil fauna populations (Critchley et al. 1979). When re-established with plantations, changed patterns and rates of accumulation of litter and the physical and chemical characteristics of the residues can lead to changes in the composition and numbers of decomposer organisms (Gosz 1984). Thus, in a comparison of soil and litter fauna under tropical rainforest and *Araucaria cunninghamii* plantations in north-eastern Australia, Holt and Spain (1986) found similar numbers of fauna in the litter layer but significantly greater numbers in soil under *Araucaria* despite the lower concentrations of organic matter on this site compared to rainforest.

Rate of decay in tropical native forests and plantations and temperate forests

In many cases litter from plantation species (Table 13.1) decays more slowly than does litter from native tropical forests (Table 13.2), especially where introduced species such as eucalypts, pines and casuarina are used in plantation establishment (Kadeba and Aduayi 1985; Spain and Le Feuvre 1987; Swamy 1989; Bargali and Singh 1991; Bargali et al. 1993; Sankaran 1993; Sankaran et al. 1993; Singh et al. 1993). Decomposition of litter from endemic species used in plantations is also often slower than litter in native forests within the same region (Brasell and Sinclair 1983; Holt and Spain 1986). Only a few studies have found similar or more rapid decomposition of litter in plantations than in native tropical forests (e.g. Bahuguna et al. 1990; Lisanework and Michelsen 1994). Annual decomposition rate constants in natural tropical forests range from 0.3 to 5.3 (Table 13.2). In tropical plantations, decay constants vary from 0.11 to 2.0 (Table 13.1). Decomposition of litter in temperate forests (Table 13.3) is usually slower than in the tropics, with annual decay constants between 0.19 and 0.68 in Australian eucalypt forests (Attiwill et al. 1978; Woods and Raison 1983), 0.3 and 0.65 in northern hemisphere pines and 0.08 and 0.47 in northern hardwoods in USA (Melillo et al. 1982).

Within the same region, litter from different plantation species varies in rate of decomposition (Table 13.1), probably due to differences in litter quality. Litter from many, though not all, nitrogen-fixing species decomposes rapidly (Tsai 1988; Swamy 1989; Binkley 1992; Bernhard-Reversat 1993), as does litter from teak (Aksornkoae et al. 1972; Egunjobi 1974; Singh and Ambasht 1980; Mary and Sankaran 1991; Sankaran 1993; Singh et al. 1993). In contrast, litter from the eucalypts (Sharma and Pande 1989; Swamy 1989; Bargali and Singh 1991; Sankaran 1993; Singh et al. 1993; Toky and Singh 1993) and conifers (Lockaby and Taylor-Boyd 1986; Gunadi 1994) often decays slowly. Low nutrient content, sclerophyllous nature, abundant crude fibres and lignin, presence of polyphenols and allelopathic chemicals in the leaves are thought to be some of the factors responsible for slow decay. For example, litter from some N-fixing species (e.g. *Acacia* and *Leucaena*), though rich in N, is slow to decay, probably because of the high lignin content of these litters (Berg et al. 1992).

Soil and litter respiration rates

Soil respiration represents the sum total of all soil metabolic activities in which CO_2 is produced, and it has been proposed as an index to monitor ecosystem response to disturbance. The three sources of the CO_2 evolved from soil are microbes, fauna and root respiration. Several factors including temperature, moisture, soil depth, soil aeration and microbial populations determine the rate of CO_2 efflux from the soil surface. In forests, microbial respiration is usually dominated by soil and litter fungi; in one study, fungal and bacterial contributions were 44% and 5.5% of total respiration, respectively (Behera et al. 1990). Although the significant contribution of the fungal component to soil respiration in tropical (Behera and Pati 1986; Behera et al. 1990) and temperate soils has been widely recognised (Anderson and Domsch 1975), the faunal contribution to soil respiration is only poorly known. Though soil invertebrates play a significant role in decomposition, their contribution to soil carbon metabolism is minimal (Edward and Sollins 1973).

The utility of CO_2 flux measurements as estimates of carbon turnover by heterotrophic organisms in litter and soil is seriously limited by our inability to accurately partition the respiratory output into its sources (Anderson and Swift 1983). In particular, the contribution of root respiration is poorly quantified and known to vary widely (Anderson et al. 1983). It was estimated to be 51% of total soil respiration in a tropical forest soil in India (Behera et al. 1990). In other tropical forests it ranges from 21% in a dipterocarp forest in Malaysia (Ogawa 1978) to 67–82% in Amazonian forests (Medina et al. 1980). These values are within the range observed for temperate forests (Anderson 1973).

The range of soil and litter respiration rates is large — 15 to 2556 mg m^2 hr^{-1} in tropical forests in general; 6 to 410 mg m^2 hr^{-1} in tropical plantations. However, the utility of these data in understanding the processes is limited because of: i) variation in experimental techniques which markedly influence estimates; ii) insufficient data to make sensible generalisations; and iii) inability to partition respiratory outputs into source components. Excluding several extreme values, 60% to 70% of the published data for temperate and tropical regions range from 100 to 500 mg m^2 hr^{-1}. These rates, usually measured over relatively short periods, are similar in the two types of ecosystems. However, annual soil respiration in many tropical forests may be higher than in temperate forests because of longer periods of warm temperatures and in some regions more favourable moisture regimes (Singh and Gupta 1977). More useful comparisons between ecosystems require studies on soil respiration, standardised methods and greater emphasis on quantifying the respiratory sources.

Nutrient dynamics during decay

Three sequential phases occur during mineralisation of nutrients from decomposing plant residues: i) an initial phase when leaching and nutrient release predominate; ii) a net immobilisation phase during which nutrients are imported into the residues by microbes; and iii) a net release phase when the nutrient mass decreases (Swift et al. 1979; Staaf and Berg 1982). However, not all these phases occur for all nutrients and all types of litter. Potassium is most mobile and a large proportion leaches out during the initial phase without immobilisation (Lousier and Parkinson 1978;

Maclean and Wein 1978; Toky and Singh 1993). Among other nutrients, Ca and Mg are often more mobile than N and P (Attiwill 1968; Baker and Attiwill 1985) and because they are often associated with cell structures, their release usually parallels loss in dry weight of the litters. Some Ca and Mg are also lost through leaching during the initial phase of decomposition (Maheswaran and Gunatilleke 1988; Ward et al. 1991) and immobilisation of Ca during later stages of decay can occur (Upadhyay 1982; Upadhyay and Singh 1989). The initial release of N and P is followed by an immobilisation phase in many types of litter in tropical, temperate and boreal forests (Wood 1974; Vitousek and Sanford 1986; Toky and Singh 1993; Lisanework and Michelsen 1994). The relative increase in N and P in decomposing litter is caused by non-symbiotic N-fixation (Granhall and Lindberg 1977), uptake from surroundings by fungal hyphae growing in litter (Berg and Soderstrom 1979), atmospheric precipitation or deposition of insect frass and plant material from the canopy. Different patterns of mobility and mineralisation of nutrient elements during decay are due to variation in carbon to nutrient ratios, nutrient requirements of decomposer organisms, resource quality, general availability of nutrients from soil, the physical environment and its effect on decomposer organisms.

Studies in temperate forests have focused on release on N and its relationship to chemical characteristics of the decaying plant residue (Berg and Staaf 1980; Aber and Melillo 1982; Gholz et al. 1985; O'Connell 1988; Aber et al. 1990). Litter properties most useful in predicting nutrient dynamics are initial N concentration and biochemical properties such as lignin and polyphenol content. Less data are available for tropical plantations and these are mostly based on incubation experiments. Palm and Sanchez (1991) compared N release from leaf materials of tropical legumes and concluded that polyphenol content of the plant residues was a better predictor of N dynamics than lignin or N content. In a greenhouse experiment (lignin+polyphenol):N ratio was the best predictor of N mineralisation from 6 types of legume residues (Fox et al. 1990). Using a wider range of residues from legumes and non-legumes, Constantinides and Fownes (1994) reported that initial N content of the materials was the variable which best predicted release or accumulation of N. Other properties such as lignin:N ratio and (lignin+polyphenol):N ratio were also significantly related to N dynamics but N concentration was most highly correlated with N mineralisation from the residues. These studies differ in their conclusions regarding the factors controlling immobilisation and mineralisation of N, probably because of the differing chemical composition of the residues and the differing experimental procedures used. Nevertheless, they do provide indications of the likely effect of a range of plant residues on N fertility of tropical soils.

Effect of Litter on Soil

Carbon distribution

On a global scale, average amounts of detrital carbon in forest soil increase from the tropics through temperate to the boreal forests (Schlesinger 1977). Low values in tropical soils are attributed to rapid decomposition which compensates for rapid litter production. However, variation within some tropical rainforests is large and can be as great as differences between tropical and temperate and boreal forests (Anderson and Swift 1983). The distribution of carbon down the soil profile also varies markedly on a global scale, with smaller amounts of detritus being stored at the soil surface in the tropics than in forests in higher latitudes. On average, about 1% of the carbon in the soil profile is stored in litter at the soil surface of tropical forests compared to 13% in boreal forests (Schlesinger 1977). At the local level, trees impact on soil chemical and physical properties and their spatial distribution. The patterns of soil properties such as pH, bulk density, organic carbon content, total nitrogen, exchangeable cations and exchange capacity are influenced by tree distribution (Ryan and McGarity 1983). This is probably due to the heterogeneous distribution of tree litter, the concentration of stemflow near the tree bole and the effect of tree roots on the soil. The geometric pattern of trees in plantation forests can be expected to be reflected in patterns of soil chemical characteristics.

Changes in soil properties when plantations are established are likely to vary between species and with characteristics of individual sites. One difficulty in interpreting the impact of individual tree species on soil fertility is the variation among results of various studies reported in the scientific literature. Specific species have been identified as having negative, positive or no effect on soil physical and chemical properties. Many of these studies are based on comparisons of adjacent or similar sites having different vegetation and in some cases the observed effects may result from inherent soil differences between the sites. Eucalypts and pines are of special interest because of their widespread application (Brown et al. 1986) in high-productivity plantations in the tropics. In one of the most detailed studies, ten plantation species were compared within one forested region with uniform soil in Puerto Rico; large differences were found between the effects of different species on storage of nutrients on the forest floor and in surface (0–10 cm) soil (Lugo et al. 1990b). This was attributed in part to the different qualities of litter of the various species. Generally as nutrient concentrations in litter increased the mass of accumulated litter decreased, suggesting faster decomposition of nutrient-rich litter. Species of pine and eucalypt had the greatest accumulations of litter while *Hernandia sonora*, a species endemic to the area, accumulated least. Soil under the pine and eucalypt stands also tended to have less organic carbon and exchangeable cations.

Bernhard-Reversat (1987) studied the role of seven introduced and natural plant species in soil organic matter formation in sahelian landscapes of the dry tropics in Senegal. On the basis of field and laboratory incubation experiments, two models of litter incorporation and soil organic matter formation were postulated. The first model, which described decay of litter from native *Acacia* species, was characterised by low levels of readily soluble compounds in fresh and partly decomposed residues, high respiratory outputs from fresh litter and a large component of organic light fractions entering the surface soil to form organo-mineral complexes. The second model, which described decomposition of *Eucalyptus* litter, was characterised by high initial levels of soluble components, moderate respiratory outputs from fresh and partly decomposed litter and low contributions of the organo light fractions to soil organic matter. It was concluded that *Eucalyptus* was unfavourable for building up soil organic matter and would result in reduced exchange capacity and decreased nutrient supply, especially in sandy soils (Bernhard-Reversat 1993). Comparisons of soil properties under teak, bombax and eucalypts in Kerala State, India support this hypothesis (Balagopalan et al. 1992). Here, soil pH, organic carbon and exchangeable bases were found to decline under eucalypt and these effects increased in magnitude with the stage of development of the eucalypt plantations. Likewise, Nandi et al. (1991) found that 14–17 yr after establishment of eucalypt plantations, soil pH, organic carbon and exchangeable cations had decreased substantially from their original values. Changes in the quality of organic matter also impact on nutrient flux rates, as evidenced by results from Senegal, which show soils under *Eucalyptus* to have low concentrations of nitrogen and reduced nitrogen mineralisation rates compared to those of native *Acacia* forests (Bernhard-Reversat 1988). Comparison of the effect of five plantation species on surface soil fertility in Puerto Rico also suggested that *Eucalyptus* added little to soil organic matter and total soil nitrogen (Wang et al. 1991). In another study Bernhard-Reversat (1991) examined changes in soil carbon under a chronosequence of eucalypt plantations from zero to 16 yr old, and confirmed the earlier finding that the eucalypts made little contribution to the organo-mineral fraction (<0.05 mm). Bargali et al. (1993) also examined organic matter dynamics in an age sequence of eucalypts, in this case *E. tereticornis* in subtropical plantations in the tarai belt of the Central Himalaya. They found decomposition was slower than in native forest, and that decay rates decreased with increasing plantation age and were associated with declining soil nutrient status. Where fast-growing, short-rotation (8–10 yr) tree crops are to be utilised for wood and fuel production rather than for revegetation and restoration of degraded land, risk of fertility decline is increased due to nutrient removal in harvested biomass. The extent of changes in soil fertility will depend on initial soil conditions, on the tree species used and on management practices applied during the period of growth and at harvest. On high quality sites, several rotations of tree crops may result in little deterioration in soil properties, but on poor sites, common in the tropics, reductions in soil nutrient status and stand productivity are likely to occur sooner unless nutrient supplies are enriched by fertilizers or from other sources.

Nutrient cycling characteristics are important selection criteria when evaluating plantation species to ameliorate land degradation problems (Lugo et al. 1990b). Where the soil environment has been degraded through loss of organic matter and nutrients, species that accumulate organic matter and nutrients in the forest floor are likely to contribute to site restoration provided sufficient time is allowed for incorporation of organic residues into soil. More nutrient-demanding species may not be so successful in such environments. Singh et al. (1989) found *Eucalyptus tereticornis* to be less suitable than *Populus deltoides* for ameliorating soil fertility in high density planting agroforestry systems inter-cropped with aromatic grasses. Nevertheless, both tree species were superior in building up organic carbon and available nitrogen and phosphorus when compared to control treatments without trees. In land degraded through alkalinity and sodicity, plantations of nitrogen-fixing species (*Prosopis juliflora* and *Acacia nilotica*) have proven to be useful in ameliorating soil problems (Garg and Jain 1992). Plantations of these trees were shown to reduce soil alkalinity and exchangeable sodium and improve the physical and chemical characteristics of the soil, probably due to input of leaf litter to the soil and the rooting patterns of the trees. Gill et al. (1987) also compared the effects of different perennial vegetation in ameliorating sodic soils, this time using *A. nilotica* and *E. tereticornis*. Growth, litter production and nutrient cycling in litter was much greater in the *Acacia* than the *Eucalyptus* plantation. It was concluded that growing acacias in plantations on highly alkaline soils will be effective in ameliorating them through lowering pH and building up organic matter and nutrients in surface soil. Eucalypts were considered to be less suitable for this purpose. *Acacia* species have also been used more generally for ameliorating degraded soils in the tropics and have been shown to successfully improve both soil physical and chemical properties (Chakraborty and Chakraborty 1989).

Interpretation of Accumulation, Decay and Mineralisation Processes

Models

The discussion so far has illustrated how individual processes such as litter accession, decomposition and accumulation, soil organic matter formation and nutrient mineralisation from organic residues are influenced by various factors such as climate, growth rates, species, site properties and stand management. Integration of these processes and interpreting their interaction with the above factors is often difficult, especially in field-based experiments where confounding effects can occur. Models provide one method for integrating process-based knowledge and for predicting the effects of factors important to long-term sustainable production from plantations. The type and complexity of models ranges from simple empirical relationships to mechanistic models which seek to describe important biologic processes in detail. In general, as the complexity of the model increases, so does the need for improved understanding and description of the functional processes and also the amount of input data needed to run the model. Here we outline some of the modelling approaches used for integrating knowledge of organic matter turnover in forests and suggest how they may be usefully applied to tropical plantations.

Stand-level carbon and nutrient models

There have been few attempts to model carbon and nutrient dynamics at the process level in tropical plantations. A budgeting approach to the stores and transfers of organic matter and nutrients has been used to describe the differences in nutrient cycles of cacao plantations with different species of shade trees (Fassbender et al. 1988) and of plantation eucalypts of different age (Bargali et al. 1992). Bormann and Gordon (1989) used a similar procedure to evaluate the impact of intensive management on nitrogen sufficiency of forests. This is a useful approach to look at the impact of harvesting on nutrient stores. However, it does not provide insight into the underlying nutrient cycling processes which is necessary for understanding the impact of different plantation species on sites or the way nutrient cycling and plantation nutrient status may vary over time and with the intensity of forest management. A more detailed mechanistic approach incorporating models of tree growth, organic matter turnover and soil nitrogen dynamics has been proposed for plantation forests (Thornley and Cannell 1992). Similar procedures have been applied in only a limited number of studies at tropical forest sites (e.g. Vitousek et al. 1994). Application of simulation models of this or similar types (e.g. Parton et al. 1988; Jenkinson 1990) to litter and soil carbon and nutrient dynamics in tropical plantations may help to elucidate some of the longer-term impacts of plantation development.

Modelling litter decomposition and accumulation

Litter decomposition is most often described by simple exponential models (Olson 1963) of the form

$$X_t = X_0 e^{-kt} \qquad (1)$$

where X_0 and X_t represent the amount of decaying residue present initially and at time t, and k is the decay constant. Models of this type generally adequately describe patterns of weight loss by residue and they also allow prediction of turnover times of organic matter. However, when applied to a heterogeneous substrate they tend to underestimate early rates of decay when more labile compounds are present and overestimate the speed of later stages of decomposition (Hunt 1977). Minderman (1968) hypothesised that during decay of plant residues, individual biochemical components are lost at a rate in proportion to the amount of each component present. Total residue decay is then described by the sum of a series of first order functions. An approximation to this proposal, the double exponential decay model (Bunnell and Tate 1974; Lousier and Parkinson 1976), has been found to provide a good description of the breakdown of a wide range of plant residues in temperate eucalypt forests (O'Connell 1987, 1994). This type of model is likely to also be applicable to tropical forests, especially those forest types which occur in regions of seasonal rainfall and where the plant residues contain substantial amounts of labile components. As well as providing better descriptions of the time course of litter decay the coefficients of these models also provide means for predicting the residence times and accumulation rates of individual litter components (O'Connell 1987). These methods have been applied in only a limited number studies of decomposition of plant residues in tropical forest plantations (Spain and Le Feuvre 1987).

Turnover time of organic residues in the forest floor can also be estimated by a mass balance approach relating rates of annual litterfall to amounts of litter accumulation at the soil surface (Olson 1963) according to the following relationship:

$$X_t = (L/k).(1\text{-}e^{-kt}) \qquad (2)$$

Where L is annual rate of litterfall. Most often it is assumed that accumulation of the forest floor has reached an equilibrium value, X_{ss}, and Equation 2 can then be rearranged and simplified to:

$$k = L/\ X_{ss} \qquad (3)$$

The forest floor is likely to reach equilibrium more rapidly in most tropical ecosystems than in temperate forests because conditions are more favourable for decomposition of organic residues. Nevertheless, there are many example in the literature where Equation 3 has been applied to litter dynamics in forests where steady-state conditions have not been established. In such cases it is likely that rates of organic matter turnover have been overestimated. These difficulties may apply in many short-rotation plantation forests, especially where litter decomposition is slow, as for some introduced species, or where rates of litterfall vary with time, as commonly occurs as young stands develop.

Differences in rates of decomposition have been related to substrate quality using various indices of decomposability. Factors used in these indices include the relative amounts of labile and recalcitrant materials, the nutrient content of tissue, the presence of inhibitory substances and the concentration of biochemical components such as lignin and cellulose (Swift et al. 1979; Schlesinger and Hassey 1981;

Melillo et al. 1982; O'Connell 1987; Aber et al. 1990). Some of the attributes have been included in generalised statistical procedures for predicting rates of decomposition on a regional or global scale. For example, Meentemeyer (1978) proposed a model of litter decomposition based on actual evapotranspiration (AET) and substrate lignin content. This approach was extended to other climatic variables in studies of litter decay in Central Himalayan forests (Upadhyay and Singh 1989; Upadhyay et al. 1989). However, although these concepts are attractive, their utility in application to a broad range of environments is still problematic due to the complexity of the biological, edaphic and climatic factors which are likely to affect decomposition processes at particular sites (Whitford et al. 1981; Anderson and Swift 1983; Parsons et al. 1986).

Nutrient dynamics

There have been only limited attempts to model nutrient release during the decay of organic residues and to predict rates of supply of soil nutrients in tropical forests. Constantinides and Fownes (1994) related N mineralisation from a wide range of organic residues to composition as described previously, but the derived predictive models were based on laboratory incubation studies and remain to be tested in the field. Empirically based models of soil organic matter and nitrogen dynamics such as the CENTURY model (Parton et al. 1988) have been applied mainly in temperate agricultural systems. This approach, which nominally separates organic matter into several separate pools, balances simplicity with enough detail to provide an understanding of system behaviour. Parton et al. (1994) evaluated CENTURY for a range of twelve tropical ecosystems, including two plantation forests, and reasonable correlations were obtained between observed and simulated productivity, soil organic carbon and soil nitrogen. Models of this type may be particularly useful in evaluating the long-term effects on soil fertility of land use such as short-rotation tree cropping. The challenge for researchers is to adequately characterise tropical forest soil and plant systems to run the model and to evaluate the model assumptions and outputs under tropical climatic conditions (Motavalli et al. 1994). Establishment of well designed long-term experiments covering a range of forest types, geographic regions and forest management treatments are crucial for this purpose. These *Type-1* experiments (Sanchez et al. 1985) would also provide a sound scientific framework for other process-based studies.

Management of Litter and Soil Organic Matter in Tropical Plantations

Role of litter and soil organic matter

Organic matter plays a crucial role in plant growth through its effect on the physical, chemical and biological properties of soils (Syers and Craswell 1995). These factors in turn influence soil structure, infiltration rates, water holding capacity, the pools of plant-available nutrients in soil and the rates of mineralisation of organically-bound nutrients. Replacement of one vegetation type with a new species, as occurs when plantations are initially established, leads to changes in the nature and level of soil organic matter and other soil properties and processes important to sustainable plant growth. Likewise, within a single vegetation type such as a forest plantation, opportunities exist to manipulate soil organic matter through silvicultural practices. This is especially so where stands are intensively managed over short rotation periods.

Organic matter and nutrient partitioning

Establishment of plantations may affect carbon allocation, the partitioning of organic matter within ecosystem compartments such as to litter, roots, and above-ground biomass and biogeochemical nutrient cycling. Only limited data exist for root distributions of tropical tree species (Chapter 8). For plantations, fine-root biomass (<2 mm) in a range of species varies from 0.26 to 2.1 t ha^{-1} (Table 13.6). Fine-root biomass in a range of natural tropical forests is greater (<1 to 8.4 t ha^{-1}, Visalakshi 1994) but variability is large and the number of studies limited. In one of the few experiments to directly compare root distributions of plantation species with natural forest, Lugo (1992) examined secondary subtropical wet forest and plantations of pine (*Pinus caribaea*) and mahogany (*Swietenia macrophylla*) established at the same sites in Puerto Rico. He found that in secondary forest a much larger proportion of fixed carbon was allocated to roots than in the plantations. Furthermore, while nutrients cycled more rapidly through decomposition of litter in the secondary forest, the plantations species showed greater nutrient-use efficiency (NPP per unit of nutrient uptake). Similar patterns were reported for Amazonian caatinga forest in Venezuela (Herrera and Jordan 1981). Comparison of natural subtropical rainforest with replacing *Eucalyptus grandis* forest in Australia (Turner and Lambert 1989) also indicated greater biomass production, higher nutrient-use efficiency and greater accumulation of forest floor mass in the eucalypt forest. In some plantations the amounts of nutrients accumulated in forest floor litter are a significant proportion of the biotically-active nutrient pool. For example in Puerto Rico, nutrients stored in the forest floor of ten plantations (age 26 yr) were similar to the amounts in surface (0–10 cm) soil (Lugo et al. 1990b). Very large accumulations

Table 13.6 Fine root biomass in tropical plantations

Species	Age (yr)	Location	Sampling depth (cm)	Diameter (mm)	Root biomass (t ha^{-1})	References
Tectona grandis	19	Varanasi, India	0–40	≤ 2	0.38–2.1	Singh and Srivastava 1985
T. grandis	29	Varanasi, India	0–40	≤ 2	0.40–1.8	Singh and Srivastava 1985
Shorea robusta	13	Meghalaya, India	0–50	> 1–2	0.26	Singh 1983
S. robusta	15	Meghalaya, India	0–50	> 1–2	0.32	Singh 1983
S. robusta	17	Meghalaya, India	0–50	> 1–2	0.49	Singh 1983
S. robusta	19	Meghalaya, India	0–50	> 1–2	0.30	Singh 1983
Eucalyptus tereticornis	2.3	Dehra Dun, India	0–120	< 2	0.27	Dhyani et al. 1990
Leucaena leucocephala	2.3	Dehra Dun, India	0–120	< 2	0.43	Dhyani et al. 1990
Eucalyptus camaldulensis	2	Morogoro, Tanzania	0–100	< 2	0.64	Jonsson et al. 1988
E. tereticornis	2	Morogoro, Tanzania	0–100	< 2	0.53	Jonsson et al. 1988
L. leucocephala	2	Morogoro, Tanzania	0–80	< 2	0.62–0.74	Jonsson et al. 1988
L. eucocephala	6	Morogoro, Tanzania	0–80	< 2	1.30	Jonsson et al. 1988
Cassia siamea	2	Morogoro, Tanzania	0–80	< 2	0.78	Jonsson et al. 1988
Pinus caribaea	11	Puerto Rico	0–30	≤ 2	1.00	Cuevas et al. 1991

of nutrients in litter and surface soil also occur where *Casuarina equisetifolia* plantations are used in afforestation of sand dune systems in Senegal (Mailly and Margolis 1992). Lugo et al. (1990a) suggest that the greater amounts of litter and the greater ratio of litter to aboveground biomass in plantations relative to natural forests is a fundamental difference between these forests in the tropics. In some circumstances the accumulation of substantial quantities of nutrients in the litter layer of plantations can act as a storage buffer against nutrient loss. At many sites, conservation of the litter layer during forest management operations, including stand harvesting, will be critically important for meeting the nutritional demands of subsequent rotations (Lugo et al. 1990b; Mailly and Margolis 1992; Chapter 15).

Use of N-fixing plants in plantations

Sustainability of intensively managed plantations depends on maintenance of adequate nutrient supply rate in the longterm. Simple budgeting models (Bormann and Gordon 1989) suggest that, to be self sufficient in N, short-rotation tree crops should contain an active biological N-fixing component. Myers et al. (1994) suggest that manipulation of mineralisation rates through mixtures of plant residue with varying qualities could form the basis of practical management systems for efficient use of nutrients and for minimising losses. Undercover crops of legumes provide one option for manipulating organic residue quality. These management practices are used routinely in many rubber plantations (Myers et al. 1994) and have also been applied in temperate conifer plantations (Gadgil et al. 1984; Nambiar and Nethercott 1987). Such procedures are also used in rubber and palm oil plantations in Malaysia where leguminous cover plants effectively reduce soil exposure during the early stages of plantation establishment (Sanchez et al. 1985). Use of mixed-species plantings incorporating endemic or introduced nitrogen-fixing plants show promise for developing productive plantations in the tropics (Ghosh et al. 1989; Binkley et al. 1992). Other understorey species may also play an important role in nutrient cycling in plantations. For example, in Puerto Rican forests (Lugo et al. 1990b; Lugo 1992) native species invade plantations and contribute significantly to nutrient cycling processes through rapid breakdown of nutrient-rich litter. However, in environments where soil moisture deficit is likely to affect plant growth, either because of limitations in total soil water storage or because a seasonally-dry climate restricts water supply at certain times of the year, ground cover or understorey vegetation can adversely affect growth of the tree crop. Thus, although the undercover crop may improve site nutrient status, especially nitrogen where legume plants are utilised, competition for soil moisture between overstorey and understorey plants may induce tree water stress and limit plantation growth. This may be especially so where understorey vegetation is dominated by woody perennial species which utilise the soil water resource continuously. Where annual crops are used as N-fixing species, induced water stress may be reduced if growth and water use of the undercover crop is predominantly during the wet season when available soil moisture is high (Nambiar and Sands 1993). Consequently, for successful use of N-fixing plants in plantations consideration of both nutrient and water requirements of each species is necessary, especially in those environments where moisture limitations are likely to restrict growth. The critical issues relevant to planting mixtures of tree species are discussed in Chapter 9.

Impact of site disturbance and harvesting on site nutrient capital

Distribution of nutrients between different tissues can have a marked influence on nutrient removal during plantation harvest and also on the addition of nutrients from harvest residues to the forest floor and soil (see Chapters 10 and 11). Nutrient concentrations generally decline in the order leaves > bark > branch wood > bole wood, although the greater mass of bole wood usually means that a large proportion of the aboveground pool of nutrients is stored in this component. Nevertheless, harvest practices which remove only bole wood will be less demanding on site nutrient capital than harvests which remove boles and branches or whole-tree harvesting. Removal of forest floor litter also has the potential to affect site fertility although little is known about the nutrient drain caused by this activity (Mao et al. 1992; Gunadi 1994). The nutrient cost of harvesting varies markedly between plantation species. For example, species of *Casuarina* and *Eucalyptus* produce more biomass per unit of nutrients than *Leucaena* spp. and *Albizia*. *Casuarina* also accumulates large amounts of nutrients in litter and adds significantly to surface soil organic carbon and nitrogen stores (Wang et al. 1991; Chapter 10). Protection of these compartments during and following harvest operations will favour retention of site nutrient capital.

Disturbance by other management practices such as fire and application of fertilizers also affects both the stores and fluxes of nutrients. Fire is one option for site preparation both at plantation establishment and to clear harvest residues between successive plantation crops. Although clearing of native tropical forests, often using slash-and-burn practices, may result in an initial pulse in the level of available plant nutrients it can also cause immediate and severe losses from the total store of these elements as well as a decline in soil organic matter (Nye and Greenland 1964; Herrera and Jordan 1981; Tiessen et al. 1994). Likewise, removal of harvest residues using fire will cause immediate volatilisation of some nutrients, especially N, and can create conditions where further loss may result through runoff, leaching and erosion. In some temperate forests regular fire has also been shown to reduce biological mineralisation rates of elements such as N (Raison et al. 1993). Application of fertilizers will be necessary to maintain sustainable production from many tropical plantations (Chapter 11). These practices can influence the nutrient flux rates, especially in litterfall and mineralisation through organic matter turnover (O'Connell and Grove 1993; O'Connell 1994). However, the impact of fertilizer additions on nutrient cycling processes and on long-term soil fertility in tropical plantations has been little studied (Smethurst and Nambiar 1990a, 1990b).

Synthesis

All forests, including plantations, are dependent on recycling of plant nutrients to meet nutrient requirements for growth. Biogeochemical nutrient cycling is, for most elements, dominated by litter production and decomposition. During litter breakdown, release of plant nutrients occurs principally through microbially-mediated biochemical reactions. Mineralised nutrients are available for uptake by the plant community. Nutrients may also be immobilised in the microbial biomass or by reactions with soil minerals or be lost from the ecosystem through leaching or in volatile forms. The primary factors affecting rate of organic residue decay and nutrient mineralisation are the nature of the plant residues, the micro-environment at the soil surface and the qualitative and quantitative composition of the decomposer organisms. Each of these factors is influenced by the tree species used for plantation establishment and by the silvicultural practices used in plantation management.

Species of *Eucalyptus* and *Pinus*, which make up about one quarter of the total area of tropical plantations, generally have higher nutrient-use efficiencies (carbon gain per unit of nutrient taken up), and produce litter that has lower concentrations of nutrients than most native tropical trees and other common plantation species. Litter in plantations of *Eucalyptus* and *Pinus*, and other genera such as *Casuarina*, usually decays more slowly and accumulates on the forest floor to a greater extent than detritus in native tropical forests. The distribution of carbon within ecosystem compartments and its effect on rates of nutrient cycling appears to be a major difference between these genera and many native tropical forests. Nitrogen-fixing trees have litter that is richer in nutrients than that of *Eucalyptus* and *Pinus* species. However, even some nitrogen-fixing trees (e.g. *Acacia auriculiformis*) produce litter which is slow to decay and which accumulates in substantial amounts on the forest floor early in the life of a plantation.

Some genera (e.g. *Eucalyptus*, *Pinus* and *Casuarina*) used in establishment of tropical plantations often accumulate a greater amount of nutrients in the litter layer than do natural forests. Slow decay of litter and the resultant immobilisation of nutrients are the main causes for the high nutrient accumulations in the forest floor. At some sites, this could induce nutrient limitation for tree growth as the plantations age due to slow turnover in accumulating forest litter. Accumulated litter is a valuable source of nutrients for growth of subsequent rotations of trees and for long-term site productivity. Silvicultural practices used during site preparation for new planting will be critical for conservation of this resource at the site.

Vegetation species can affect the rate of litter decomposition and consequently modify soil organic matter formation and the rate of biogeochemical nutrient cycling. Trees with high nutrient-use efficiency (NPP per unit of nutrient uptake) such as *Eucalyptus*, *Pinus* or *Casuarina* will place lower nutrient demands per unit of production on the site than will more nutrient-demanding species. They also produce litter which has low concentrations of some plant nutrients and which decays slowly. Slow litter turnover and mineralisation of organically-bound nutrients can lead to reductions in soil organic matter and site fertility over time. Silvicultural practices used in management of plantations can impact significantly on these processes. A range of options is available to forest managers to conserve soil organic matter and reduce nutrient drain and perturbations to nutrient cycling processes, especially during the inter-rotation period (see Chapter 10). In many regions, some inputs of nutrients in fertilizers or from other sources will also be necessary to maintain site nutrient capital and sustain plantation productivity in the long term, especially where short-rotation tree cropping is practised (Chapter 11). There is a need to better understand the impact of intensive management practices on the storage and fluxes of plant nutrients. We consider this to be a priority for research in tropical plantations, especially where short rotations are used.

Nutrient cycling characteristics are important selection criteria when evaluating plantation species for certain sites. If restoration of degraded land is the main purpose of plantation establishment, species which have efficient nutrient cycles, and which enrich soil with organic matter and nutrients are the best options. Nitrogen-fixing trees and shrubs such as *Acacia*, *Casuarina*, *Albizia*, *Leucaena* and *Alnus*, when established in plantations either alone or in mixtures with other species, can serve an important role for maintaining and enhancing site nutrient status in short-rotation wood production plantations (Chapter 9). Use of more than one species, either in the tree stratum or as undercover crops, also provides possibilities for modifying the patterns and supply rates of soil-stored nutrients, and manipulating mineralisation rates through mixtures of plant residue (organic matter) with varying qualities.

Simulation modelling provides one means of integrating knowledge on nutrient cycling and assessing the likely effects of intensive forest management practices. There has been only limited use of these techniques for evaluating long-term responses of soil carbon and nutrient storage and flux rates to changed land management in the tropics. Models such as CENTURY, adapted for use in tropical forests, may prove useful for this purpose. Simulations from such models may provide insights into the changes in soil organic matter and soil fertility that are likely to result from specific land use and land management practices. Consequences of various alternative practices can be rapidly explored through model simulations as a basis for selecting specific land management options and/or experimental treatments in research programs. Validation of the predictions of such models is dependant on establishment of well designed long-term experiments covering a range of forest types, geographic regions and forest management treatments. These sites would also provide a sound scientific framework for other process-based studies.We consider that further development of simulation models together with their application to understanding the effect on soil fertility of establishment and intensive management of plantations in the tropics to be an important area for future research.

Acknowledgments

This review was written during the tenure of a Darwin Fellowship by the junior author at the International Mycological Institute (IMI), U.K., awarded by the U.K. Department of the Environment. He is grateful to Dr S. Chand Basha, Director, Kerala Forest Research Institute for granting the necessary study leave and to Dr B.C. Sutton, Assistant Director, IMI, for encouragement. Extensive assistance with literature searches and other library services provided by Bernadette Waugh and Linley Thornber at CSIRO and Liz Wheater at IMI is gratefully acknowledged. Special thanks are due to Dr Jerry Cooper, Computing Manager, IMI for facilitating electronic information transfer between the authors. Help from several colleagues at the Kerala Forest Research Institute is also gratefully acknowledged.

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14

Reforestation of Salt-affected and Acid Soils

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Abstract

Human-induced land degradation has resulted from intensification of agricultural practices and from destruction of forest ecosystems. In addition many soils are naturally infertile or physically difficult to cultivate. In this chapter we deal with reforestation of salt-affected and acid soils only, even though other types of degraded land, such as eroded or ex-mining sites, may present opportunities for commercial tree growing and rehabilitation. Salt-affected and acid soils occur over several thousand million hectares of land worldwide. When suitable tree species are used and appropriate land management practices are employed, these soils can afford opportunities for sustainable plantation and farm forestry. Considerably more effort is required to increase the sustainable productivity of salt-affected than acid soils. Critical soil, plant and management factors that have a strong influence on reforestation strategies are discussed, with a particular focus on tropical and subtropical regions.

LARGE AREAS of agricultural and forest land have become degraded in many tropical and subtropical areas of the world. Much of this land will require remedial action before productive, sustainable land-use systems, including plantation forestry, can be developed. For the purpose of this paper, the term land degradation is used to denote the deleterious changes to the land resource, such as reduced soil fertility, loss of topsoil and loss of plant species diversity, which result in decreased growth of crops, pastures and trees. The term degraded land is still somewhat subjective when viewed from a socioeconomic perspective; its meaning may differ among various land use groups, e.g. rural and urban inhabitants.

The results of a Global Assessment of Soil Degradation (GLASOD), based on the World Map of the Status of Human-Induced Soil Degradation (Oldeman et al. 1991), indicate that almost 2000 million (M) ha of land have been affected by land degradation processes over the past five decades. The four major types of land degradation processes are: i) water erosion (1094 M ha); ii) wind erosion (548 M ha); iii) chemical soil deterioration (239 M ha); and iv) physical soil deterioration (83 M ha).

Five different causes of physical human intervention have been identified that have resulted in soil degradation (Oldeman et al. 1991). These are: i) deforestation and removal of natural vegetation (579 M ha); ii) overgrazing of vegetation by livestock (679 M ha); iii) improper management of agricultural land (552 M ha); iv) over-exploitation of vegetation for domestic use (133 M ha); and v) (bio) industrial activities leading to chemical pollution (23 M ha). Of these, i) and iii) are of direct interest for this chapter. Four degrees of soil degradation are recognised (Oldeman et al. 1991): i) light (749 M ha); ii) moderate (910 M ha); iii) strong (296 M ha); and iv) extreme (9 M ha). Commercial forestry and various types of agroforestry operations can, in principle, be contemplated for lightly and moderately affected areas, because these areas require relatively simple management.

Increasingly, the landscape of the tropics consists of vast areas of cleared or shrub-covered lands interspersed with relic patches of forest. Deforestation has resulted from land clearing for agriculture, forest products and other pursuits, including mining. Restoration of degraded land is often attempted with fast-growing tree species with the aim of satisfying community demand for wood products, minimising incursions into natural forest and allowing establishment of native forest species following amelioration of soil conditions. The use of fast-growing exotic species is often linked to short-term considerations such as early production and financial returns (Nair and Chand Basha 1995). These goals can provide important economic incentives for tree growing and may enhance the rate of site restoration. However, as pointed out by Parrotta (1992), Nair and Chand Basha (1995) and others, appropriate emphasis should be given to the use of site-specific indigenous species if diversity-linked ecosystem redevelopment is to take place and provide longer-term stability for plantation and farm forestry.

There are some key constraints to the establishment and growth of trees on degraded land. These are: i) deficiency of nutrients; ii) high concentrations of toxic elements and compounds; iii) high soil compaction and soil strength and iv) low activity of symbiotic micro-organisms. Correct choice of trees and symbionts is essential for successful establishment of plantations but survival and growth are also markedly improved by the use of specific cultural practices and amendments.

This chapter focuses on reforestation of salt-affected and acid soils. The following issues are dealt with in detail: i) characteristics and processes in saline, sodic and acid soils; ii) physiological processes in and adaptation of plants to these soils; iii) screening and evaluation of tree genotypes; iv) techniques for tree establishment and growth; v) relationships between productivity and key soil properties, and vi) prospects for site rehabilitation by tree growing. Wherever possible, the influence of specific stress factors are related to general principles governing both tree growth and plantation establishment and management in relation to water and nutrients discussed in earlier chapters. Effects of waterlogging are also discussed since this condition, resulting from either seasonally-high rainfall, excessive irrigation or both, can occur on both salt-affected and acid soils.

Reforestation of Salt-affected Land

Approximately 1000 M ha or 7% of the world's land area is salt-affected (Dudal and Purnell 1986). Of this area, more than 76 M ha has become salt-affected due to human impacts on land use. Worldwide there are 52.7 M ha in Asia, 14.8 M ha in Africa, 4.4 M ha in America and 3.8 M ha in Europe (Oldeman et al. 1991). In Australia, there are over 4 M ha of salt-affected soils (Williamson 1990). Estimates given by Dregne et al. (1991) agree well with the above, suggesting that about 74.2 M ha are salt-affected; of this, 43 M ha is irrigated land in the world's semi-arid and arid regions and 31.2 M ha is secondary salinised non-irrigated land. Secondary salinisation has resulted through inappropriate water management in a variety of landscapes, e.g. by over-irrigation in semi-arid climates (Szabolcs 1989) and by clearing of deep-rooted native vegetation in rainfed areas (Schofield 1992).

Salt-affected soils are usually found in countries with: i) seasonally-dry tropical climates (e.g. Thailand, Sri Lanka); ii) semi-arid and arid climates (e.g. Pakistan, northern India, Australia) or semiarid coastal climates (e.g. Thailand, India, Sri Lanka). In addition, many countries, such as India and Indonesia, have coastal mangrove ecosystems that can be sustainably utilised for fuelwood, crustaceans and other resources (Untawale 1985).

Characterisation of and processes in salt-affected soils

Classification of salt-affected soils varies widely (Szabolcs 1989). The FAO/UNESCO classification recognises: i) solonchak soils, which have high salt concentrations; ii) solonetz soils, which have high exchangeable sodium; and iii) saline and sodic phases of other soil groups (Dudal and Purnell 1986).

The source of the excess soluble salts in soil profiles may be one or more of the following (Hingston and Gailitis 1976; Chaudary et al. 1978; Sheikh 1987; Abrol et al. 1988):

(i) cyclical salts, blown inland and deposited with rainfall, often hundreds of kilometres inland, over long periods (e.g. in Western Australia),

(ii) large salt deposits from the original parent material during soil development (e.g. soils in arid areas of the Indus Basin in Pakistan; western Rajasthan in India),

(iii) salts contained in irrigation water (e.g. in saline groundwater pumped from tubewells) or lost in conveyance through irrigation water distribution systems,

(iv) salts in water inflow (seepage) from upland areas diverted to landscape depressions by impermeable horizontal layers, under dryland conditions (e.g. southern Australia), and

(v) salts deposited through the upward movement (capillary action) of water from shallow groundwater tables (e.g. Indus Basin in Pakistan and southern Australia).

The higher the soil evaporation rate and the more saline the watertable, the greater will be degree of salinisation. The critical depth to the watertable from which significant upward capillary water movement is possible varies from approximately one metre in heavy, slowly-permeable clays to several metres in highly permeable loams.

The amount of soluble salt in the soil profile may be subject to considerable temporal and spatial variation. The depth to and salinity of the groundwater table are usually of primary importance in determining the potential for salinisation of the upper soil profiles. Heterogeneity of soil salinity is associated with: i) changes in microtopography; ii) rates of infiltration of water governed by texture, structure and sodium (Na) concentration; and iii) rates of capillary rise of water containing salt. Where pronounced dry and wet seasons occur, both watertable and surface soil salt concentrations can vary markedly, salt concentrations typically rising with increasing evaporative demand in hot, dry seasons.

Salt-affected soils have been adversely altered for the growth of most plants by the action or presence of soluble salts (saline soils), the exchangeable Na percentage (sodic or alkali soils) or both (saline-sodic soils). A summary of properties of these soils and major factors impacting on plant growth is presented in Table 14.1.

Saline soils contain high concentrations of soluble salts (usually chloride (Cl) or sulfate (SO_4) salts of Na, magnesium (Mg) and calcium (Ca)), commonly at or close to the surface, sufficient to reduce survival and growth of most plants. Criteria for assessment of salinity classes have been given by Richards (1954). The most appropriate measure of soil salinity is EC_e (electrical conductivity of water extracted from a saturated soil paste). Other often-used units such as $EC_{1:5}$, parts per million and percent salt can be converted to EC_e through the use of appropriate equations (Richards 1954).

Low soil Ca concentrations will usually aggravate effects of salinity. In contrast to saline soils, sodic soils contain sufficient exchangeable Na (i.e. Na-occupied negatively charged exchange sites on soil colloids (silt and clay)) to adversely affect soil physical properties, particularly soil structure, infiltration and aeration (Yadav 1989). Sodic soils develop after repeated alternate wet and dry seasons when divalent cations precipitate from the soil solution and the proportion of Na ions increases, or when shallow groundwater with high Na concentrations is present (Abrol et al. 1988). Excessive Na deflocculates soil colloids, and causes very low infiltration rates and poor hydraulic conductivity, and impedes drainage through soil. Rainwater will often pond on the soil surface for long periods. The most appropriate measure of sodicity is the percentage of exchangeable Na relative to exchangeable Ca and Mg, i.e. the exchangeable sodium percentage (ESP). The presence of a compact calcic horizon (calcium carbonate concretions or kankars),

Table 14.1 Major properties of saline, sodic, acid and waterlogged soils relevant to tree survival and growth

Property	Saline	Sodic	Acid	Waterlogged
ECe	> 2–4 dS m^{-1} [a]	< 2–4 dS m^{-1}	< 2–4 dS m^{-1}	n.a.[b]
ESP	< 15	> 15 [c]	Usually < 15	n.a.[b]
pH	< 8.2	> 8.2	< 6.5	pH fluctuations
Major products	Na, Cl, SO_4 predominate	Na, CO_3, HCO_3 predominate	Al [d], Mn [d]predominate	Anaerobic respiration end products
Physical structure	Flocculated	Dispersed	Usually flocculated	Variable: low O_2 concentrations
Soil water	Osmotically-induced water stress likely	Reduced access to subsoil moisture likely due to impeding layers	Reduced access to moisture likely due to high Al-induced curtailed root growth	Excess supply
Essential nutrients	Imbalance	Imbalance	Imbalance	Imbalance
Other	Often high Na:Ca	High Na:Ca	High Al:Ca	n.a.[b]

[a]dS m^{-1} = deci seimens per metre; [b]not applicable; [c]under Australian conditions (sodic soils have ESP > 6); [d] Al (aluminium), Mn (manganese)

often present in sodic soils, will severely restrict root penetration and movement of water and air within the soil profile (Abrol et al. 1988).

The effects of Na are modified by the salinity of the soil solution. In combination with salinity (i.e. saline-sodic soils), Na has less effect on soil structure than without salt. Soil structure and permeability may remain stable at high ESP provided the irrigation water contains sufficient salt. As the soil ESP increases, the minimum salt concentration of the irrigation water required to maintain stable soil permeability also increases (Ayers and Wescot 1985).

The pH of saline and saline-sodic soils can fluctuate markedly with season. For example, in northeast Thailand soil pH rises to 8–9 in the wet season (when Na is solubilised) and falls to values of 2–3 in the dry season (Mitsuchi et al. 1986). Acid-sulfate soils, which often occur in tidal swamps, have low pH (3–4) as well as high levels of salinity. Such large pH shifts are likely to impact significantly on nutrient availability.

Waterlogging may result when soils are poorly drained (as may be the case with sodic soils) or underlain with a shallow watertable. Watertables will be at their highest during the hot monsoon seasons. Saline-sodic soils may become saturated at or near to the surface and may be inundated for weeks or months; this may also be the case with saline soils which have no or limited subsurface drainage (Ansari and Khanzada 1995). If a sufficiently large proportion of the root zone is saturated for long periods, there may be insufficient soil oxygen to support normal root growth. However, development of reduced oxygen conditions in soils is usually nonuniform; thus plants may be subjected in all or part of the root zone to conditions ranging from fully air-saturated to anaerobic (Drew 1983).

Waterlogging may interfere with normal mineral nutrition of plants causing poor plant health. For example, reduced N uptake can lead to leaf senescence. The impact of waterlogging on sodic soils may be particularly severe since these soils are already nutritionally unbalanced. Nutrient availability to plants can also be modified in waterlogged soils due to microbially-mediated reduction processes which occur at lower redox potentials. For example, N levels can be lowered due to denitrification of nitrate ($N0_3$) to nitrogen (N_2) gas, and soluble Mn and Fe can be increased to toxic levels. Tree plantations established on saline-sodic, seasonally-waterlogged soil often display a variety of foliar symptoms resulting from nutrient imbalance (Fig. 14.1).

Naturally saline-sodic soils may become sodic soils when leached with low-salinity irrigation waters. If Na, bicarbonate and/or carbonate ions are present in the irrigation or groundwater the soil may become saline, sodic and alkaline. When more than one factor is limiting, careful management is necessary.

Figure 14.1 Foliar symptoms of nutrient imbalance. *Eucalyptus camaldulensis* from a local seed source, six months old, planted on moderately-high saline, sodic farmland near Faisalabad, Pakistan. (Photo: N.E. Marcar)

Use of salt-affected soils for tree plantations

Depending on the severity of salt-affected land, there are several options for establishing vegetation or changing the type of vegetation. Use of perennial plants has the advantage of reducing annual maintenance costs and their deeper-rooted habit will assist with water management which is the key to salinity control. Extremely salt-affected and bare land needs to be revegetated with halophytic plants such as *Atriplex* species (Malcolm 1993). As conditions become less severe, it will be possible to plant nonhalophytic trees, shrubs and grasses. In less severe cases it will also be technically possible and may be economically feasible to further reduce salinity and waterlogging by soil and water management in order to grow commercial crops.

Salt-affected soils in the tropics can be used for small and large-scale fast-growing plantations and farm and community forestry, but to achieve sustained high productivity a number of soil- and plant-based management practices are needed.

Tree evaluation, selection and improvement

There are three major constraints to the growth of plants exposed to saline conditions: i) water deficit (drought stress) arising from the low (more negative) soil water potential; ii) ion toxicity associated with excessive uptake mainly of Cl^- and Na^+; and iii) nutrient imbalance due to depressed uptake and/or shoot transport and impaired internal distribution of mineral nutrients (Greenway and Munns 1980).

In addition, excessive waterlogging and low concentrations of specific nutrients (e.g. Ca) are likely to aggravate effects of salinity by impairing the functioning of root membranes, thereby reducing the ability to selectively absorb potassium (K) in preference to Na (Greenway and Munns 1980).

Mechanisms of salt and waterlogging tolerance

A variety of mechanisms contribute to differential tolerance of tree species to salinity and waterlogging.

Several tree species, such as *Prosopis* spp. and *Tamarix* spp., occur naturally on salt-affected soil. These species, termed halophytes, have evolved several salt-tolerating mechanisms. Halophytes tend to show growth stimulation at low levels of salt but growth reduction at higher concentrations (Greenway and Munns 1980). Adaptations include increased leaf succulence, subcellular regulation (in vacuoles) of absorbed salt ions in leaves and salt excretory glands on leaves (e.g. *Tamarix aphylla).* Utilising salt for osmotic adjustment is the only mechanism which exploits the saline environment and which results in the maintenance of plant water potentials and growth at high salinities (Yeo 1994). Nevertheless halophytes can regulate the rate of entry and the type of ions absorbed by roots and transported to the shoots. Some halophytic-type plants also restrict the uptake of salt at relatively low salinities, as is the case with *Acacia ampliceps* (Marcar et al. 1991a).

Most tree species are nonhalophytes, i.e. they do not grow well on highly salt-affected land. Non-halophytes rely on avoidance mechanisms that include restricting the entry of salt into the root and transport in the xylem and retaining most of the salt that enters the shoot in old leaves (Yeo 1994). One of the most important effects of salinity in the short-term is to reduce leaf expansion, probably as a result of hormonal signals emanating from roots due to altered root water status (Munns and Termaat 1986). In the longer-term, the ability of fully expanded leaves to deal with high intra-cellular salt concentrations is most important (Munns and Termaat 1986). Progressive loss of leaves through excessive ion accumulation will ultimately lead to plant death (Greenway and Munns 1980; Munns 1993).

Adaptations to waterlogging include development of aerenchyma (air-filled) tissues within primary and lower order roots near the soil surface, and extensive lateral root systems, to maximise oxygen uptake and release of potentially toxic gases such as ethylene (Pereira and Kozlowski 1977).

Evaluation for salt tolerance

Several tree species occur naturally within or near to coastal or inland sites where soils or groundwaters are saline. For example, in southeastern Australia *Melaleuca* spp., *Eucalyptus botryoides*, *E. robusta* and *Casuarina glauca* fringe coastal saltmarshes, estuaries and lagoons (Adams 1995). Stands of *Acacia auriculiformis* and *A. aulacocarpa* occur next to mangroves on river banks in coastal Papua New Guinea (M. McDonald, pers. comm.). It might be expected that species which have evolved in saline habitats will have acquired more salt-tolerating characteristics. This is often but not always the case. For example, Thomson (1988) found that the salinity level in the upper soil horizons (0–30 cm) at the place of origin in southern Australia was not closely correlated with differences in NaCl tolerance between provenances of *E. camaldulensis*.

Plantation tree species of commercial interest are all nonhalophytes and have, at best, only moderate salt tolerance. A program of screening (to capture naturally-occurring genetic variability), selection and improvement is required to increase the salt tolerance of particular species if they are required to be grown commercially on salt-affected land. Evaluation programs must include the range of stresses likely to be encountered for salt-affected sites. Complementary programs to select salt tolerant symbionts (in particular, *Rhizobium* and *Frankia)* and effective combinations of symbiont strain and tree species are also likely to be beneficial for N-fixing trees on salt-affected land (Reddell 1993).

Many glasshouse studies aimed at evaluating salt tolerance of seedlings at the species level have been reported. In these, varying concentrations of single or mixed salts are applied to seedlings in pots filled with soil, sand or potting mix, and irrigated with known volumes of treatment solution (Aswathappa et al. 1986). Waterlogging can be also be superimposed (van der Moezel et al. 1988; Marcar 1993), and oxygen concentrations and/or redox potentials can be regularly determined within each pot. Emphasis has usually been placed on survival at high salt concentrations (Aswathappa et al. 1986; Thomson et al. 1987; Rhodes and Felker 1988), but also on growth at moderate concentrations (Marcar et al. 1995a).

Identification of phenotypically-superior genetic variation during glasshouse screening can be an important first step for selecting more appropriate material for field evaluation (Thomson 1988). Significant intra-specific variation for salt tolerance has been reported for several species including *E. camaldulensis* (Thomson et al. 1987), *Prosopis* spp. (Rhodes and Felker 1988) and *E. grandis* and *E. globulus* (Marcar et al. 1995a). Based on intra-specific variation, selected glasshouse-grown plants of *E. camaldulensis* and *Casuarina glauca* with high salt and combined salt and waterlogging tolerance have been vegetatively propagated (cloned) and subsequently field-evaluated (Bell et al. 1994). Reliable information on field performance on saline sites of *E. camaldulensis* clones versus unselected seedlings from the same seed source is now emerging (Bell et al. 1994; Morris 1995). Evidence to date indicates that clones developed from plants selected under combined salt and waterlogging treatments perform better than unselected seedlings from the same seed source (Bell et al. 1994). Clones of *E. camaldulensis* developed from trees selected on saline field sites also appear to be performing better than unselected trees when planted on saline land (Morris 1995). However, *E. camaldulensis* clones developed from glasshouse-grown seedlings selected for salt tolerance alone have not performed any better on saline land than unselected seedlings from the same seed source, although clonal differences in architecture, stem form, branching habit and insect resistance have been observed (van der Moezel 1993; Bell et al. 1994; Marcar et al. 1994).

During the last few decades a number of well-designed species evaluation trials have been established on saline sites in several countries. Some of these trials include well characterised soil salinities (e.g. Pepper and Craig 1986) and a few (e.g. Marcar et al. 1994; Dunn et al. 1995) incorporate rapid assessments of soil salinities under individual trees using a hand-held electromagnetic induction device (EM38). Using this device, apparent conductivity (EC_a) values calculated for the 0–60 cm horizon (or similar depth) are converted to EC_e after determination of soil texture, water content and $EC_{1:5}$ for specific profiles spanning the range of salinity levels across the site (Slavich and Petterson 1990). This procedure provides more rigorous information compared with the use of data obtained from widely spaced soil cores, but even such procedures cannot measure the expected large temporal fluctuations in soil salinity unless very frequent measurements are made and a salinity stress index is calculated.

The information generated from such studies has been used to refine knowledge of soil salinities tolerated by tree species in the field, in terms of growth decline and survival with increasing salinity. Figure 14.2 shows three generalised relationships between tree growth and EC_e. This figure is based on field data from 5–10-yr-old trees (Marcar et al. 1995b). From such figures it is possible to estimate: i) growth in the absence of salt; and ii) the EC_e level corresponding to incipient (c. 10%) and c. 50% growth reduction. In the case of curve A (*Acacia stenophylla*) it is clear that there is stimulation of growth at $EC_e < 5$ dS m^{-1}. It is necessary that more of these relationships be developed for species that are used for reforestation.

There is only limited information on yield per unit area (as compared with plot-scale data) in response to salinity, and this gap needs to be addressed. One example is given by Bennett and George (1996) who show that mean annual volume increments (MAIs) of 10 m^3 ha^{-1} yr^{-1} on moderately saline soils in south-western Western Australia may be reasonably expected for the Lake Albacutya provenance of *E. camaldulensis*, and that EC_e of about 5 dS m^{-1} appears to be an upper limit for economically-viable wood production.

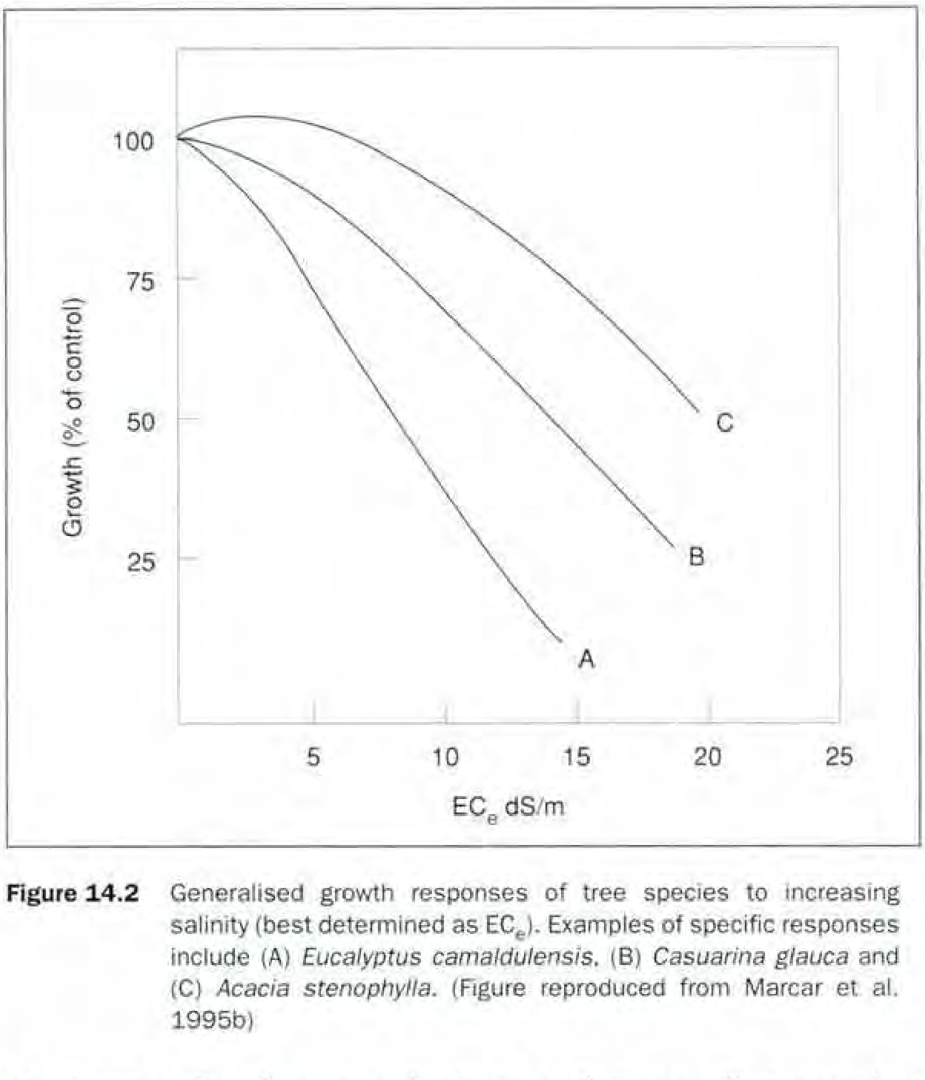

Figure 14.2 Generalised growth responses of tree species to increasing salinity (best determined as EC_e). Examples of specific responses include (A) *Eucalyptus camaldulensis*, (B) *Casuarina glauca* and (C) *Acacia stenophylla*. (Figure reproduced from Marcar et al. 1995b)

Even in these studies, however, the impact of site-specific interacting factors, such as waterlogging or water deficit, are rarely evaluated let alone isolated. For example, dramatic increases in mortality often occur on saline land which becomes temporarily waterlogged or inundated, even for highly salt-tolerant species such as *A. ampliceps* and halophytes such as *Atriplex* species (Galloway and Davidson 1992). It is also very difficult to draw general conclusions about species performances in the field since trials have been conducted over a range of climates, cultural practices (e.g. with and without gypsum addition and mounding), soil types and soil conditions (viz. saline, sodic, waterlogged and all their combinations), and tree performance reported at various ages. For example, since waterlogging interacts strongly with salinity to reduce survival and growth, it is impossible to compare data from trials which use different mounding practices.

Table 14.2 presents a list of selected tree species reported to be tolerant of varying levels of soil salinity. This table has been compiled from a wide range of published and unpublished trial information, and emphasises species suitable for the tropics and subtropics.

Table 14.2 Rating of selected tree species to moderate, high and severe levels of soil salinity, sodicity and acidity, and under waterlogging conditions. It must be noted that for several species provenances may vary considerably in growth and tolerance of the above conditions. For convenience the following categories are defined (Marcar et al. 1995b): soil salinity levels are expressed as EC_e in units of dS m^{-1} (low (<4), moderate (4–8), high (8–16), severe (>16)); soil sodicity classes are expressed in terms of pH (moderate (8.0–9.0), high (9.0–10.0) and severe (>10.0)); soil acidity classes are expressed in terms of pH (moderate (5.5–6.5), high (4.5–5.5) and severe (< 4.5)). Selected references have been given for classification of species into particular categories.

Species	Salinity (EC_e)	Acidity (pH)	Sodicity	Waterlogging
*Acacia ampliceps**	Severe [b]		Severe [b,w]	No [b]
Acacia albida		Moderate [n]		
Acacia anuera		Severe [k]		
Acacia aulococarpa		High [k,l]		
Acacia auriculiformis *	Moderate [a,g]	High/severe [h,l,m,q]		Yes [u]
Acacia crassicarpa		High [k,l]		
Acacia decurrens		Moderate [n]		
Acacia difficilis		Severe [k]		
Acacia elata		Moderate [k]		
Acacia julifera		Severe [k]		
Acacia koa		Severe [r]		
Acacia machonochiena	Severe [g]		Severe [g]	
Acacia mangium	Low [g]	Moderate/high [h,r]		Yes
Acacia mearnsii	Low [g]	Moderate [n,r]		
Acacia nilotica	Moderate [a,g]	Moderate [n]	High [a]	
Acacia salicina	High [b]		High [b]	
Acacia saligna	Moderate [a,b]		Moderate [g]	
Acacia stenophylla	Severe [b]		Severe [b,w]	Yes [b]

Table 14.2 (cont'd) Rating of selected tree species to moderate, high and severe levels of soil salinity, sodicity and acidity, and under waterlogging conditions. It must be noted that for several species provenances may vary considerably in growth and tolerance of the above conditions. For convenience the following categories are defined (Marcar et al. 1995b): soil salinity levels are expressed as EC_e in units of dS m^{-1} (low (<4), moderate (4–8), high (8–16), severe (>16)); soil sodicity classes are expressed in terms of pH (moderate (8.0–9.0), high (9.0–10.0) and severe (>10.0)); soil acidity classes are expressed in terms of pH (moderate (5.5–6.5), high (4.5–5.5) and severe (< 4.5)). Selected references have been given for classification of species into particular categories.

Species	**Salinity (EC_e)**	**Acidity (pH)**	**Sodicity**	**Waterlogging**
Acacia tortilis	Moderate [d]			
Acacia tumida		Severe [k]		
Ailanthus excelsa	High [a]		Moderate [f]	
Albizia lebbeck	Moderate [a,c]	Moderate [r]	Moderate [a,f]	
Albizia procera			Moderate [f]	Yes [u]
Alnus acuminata		Moderate/severe [n,h]		
Anthocepalus chinensis				Yes [u]
Azadirachta indica	Moderate [a,c]	High [m]		
Barringtonia acutangula				Yes [u]
Bischofia javanica				Yes [u]
Bombax ceiba				Yes [u]
Butea monosperma	Moderate [a,c]		High [f]	
Calliandra calothyrsus		High/severe [j,p]		
Callitris columellaris		Moderate [j]		
Capparis aphylla	High [a]			
Cassia siamea		Moderate/severe [j,p]		

Table 14.2 (cont'd) Rating of selected tree species to moderate, high and severe levels of soil salinity, sodicity and acidity, and under waterlogging conditions. It must be noted that for several species provenances may vary considerably in growth and tolerance of the above conditions. For convenience the following categories are defined (Marcar et al. 1995b): soil salinity levels are expressed as EC_e in units of dS m^{-1} (low (<4), moderate (4–8), high (8–16), severe (>16)); soil sodicity classes are expressed in terms of pH (moderate (8.0–9.0), high (9.0–10.0) and severe (>10.0)); soil acidity classes are expressed in terms of pH (moderate (5.5–6.5), high (4.5–5.5) and severe (< 4.5)). Selected references have been given for classification of species into particular categories.

Species	Salinity (EC_e)	Acidity (pH)	Sodicity	Waterlogging
Casuarina cunninghamiana	Moderate/high [a,b,c,e]	Moderate [r]		Yes [b]
Casuarina equisetifolia	Moderate [a,g]		High [a,f]	Yes [t]
*Casuarina glauca**	High [a,b,e]		Moderate/high [b]	Yes [b]
Casuarina junghuhniana		Moderate/high [n,r]		
*Casuarina obesa**	High/severe [b,v]		High [b,w]	
Conocarpus lancifolius	High [a,g]			
Dalbergia sissoo	Moderate [a]		Moderate/high [f]	
Eucalyptus brassiana	Moderate [g]	Moderate [l]		
*Eucalyptus camaldulensis**	Moderate/high [a,b,d,g]		High [a,b,w]	Yes [b,t,u]
Eucalyptus citriodora	Moderate [a]	Moderate		
Eucalyptus cloeziana		High [n]		
*Eucalyptus grandis**	Low/moderate [b,e]	Moderate [o]		Yes [b]
Eucalyptus coolabah	Moderate [b,g]		High [g]	
Eucalyptus moluccana	Moderate/high [b,e]			
*Eucalyptus occidentalis**	High [b]			
Eucalyptus raveretiana	High [e]	High		
Eucalyptus robusta	Moderate [e]	Moderate [k]		

Table 14.2 (cont'd) Rating of selected tree species to moderate, high and severe levels of soil salinity, sodicity and acidity, and under waterlogging conditions. It must be noted that for several species provenances may vary considerably in growth and tolerance of the above conditions. For convenience the following categories are defined (Marcar et al. 1995b): soil salinity levels are expressed as EC_e in units of dS m^{-1} (low (<4), moderate (4–8), high (8–16), severe (>16)); soil sodicity classes are expressed in terms of pH (moderate (8.0–9.0), high (9.0–10.0) and severe (>10.0)); soil acidity classes are expressed in terms of pH (moderate (5.5–6.5), high (4.5–5.5) and severe (< 4.5)). Selected references have been given for classification of species into particular categories.

Species	Salinity (EC_e)	Acidity (pH)	Sodicity	Waterlogging
Eucalyptus rudis	High [b]			
Eucalyptus tereticornis *	Moderate/high [a,b,e]	Moderate	High [g]	
Faidherbia albida		High [h]		Yes [t,u]
Grevillea glauca		Severe [i]		Yes [t]
Grevillea pteridifolia		Severe [i]		Yes [b,t,u]
Leucaena leucocephala	Low/moderate	Moderate [i]	Moderate [f]	
Melaleuca arcana	Moderate [g]	Moderate		
Melaleuca bracteata	Moderate/high [b,e]		Moderate/high [b]	Yes [u]
Melaleuca halmaturorum	Severe [b]		Moderate [g]	
Melaleuca leucadendra	High [b,g]			Yes [b]
Paraserianthes falcataria		Moderate/severe [n,s]		Yes [b]
Parkinsonia aculeata	Moderate [a]			Yes [b]
Pinus elliotti		High		Yes
Pinus halepensis	Moderate [a]	Moderate		
Pinus occidentale		High [n]		
Pongamia pinnata	Moderate [c]			
Populus euphratica	Moderate [a]	Moderate [a]		
Prosopis alba			High [g,w]	
Prosopis chilensis			High [w]	

Table 14.2 (cont'd) Rating of selected tree species to moderate, high and severe levels of soil salinity, sodicity and acidity, and under waterlogging conditions. It must be noted that for several species provenances may vary considerably in growth and tolerance of the above conditions. For convenience the following categories are defined (Marcar et al. 1995b): soil salinity levels are expressed as EC_e in units of $dS\ m^{-1}$ (low (<4), moderate (4–8), high (8–16), severe (>16)); soil sodicity classes are expressed in terms of pH (moderate (8.0–9.0), high (9.0–10.0) and severe (>10.0)); soil acidity classes are expressed in terms of pH (moderate (5.5–6.5), high (4.5–5.5) and severe (< 4.5)). Selected references have been given for classification of species into particular categories.

Species	**Salinity (EC_e)**	**Acidity (pH)**	**Sodicity**	**Waterlogging**
Prosopis juliflora	Severe [a,d,g]	Moderate [l]	High [w]	Yes [t]
Sesbania formosa	Moderate [g]			Yes [t]
Sesbania grandiflora	Moderate [a]			Yes [u]
Syzium cumini				Yes [t]
Tamarix aphylla	Severe [a,d]			Yes [g]
Tamarix articulata	Severe [a]			Yes [a]
Tamarix gallica	Severe [a]			Yes [u]
Terminalia arjuna	High [a,c]		Moderate/high [f]	
Zizyphus jujube	High [a]			Yes [u]
Zizyphus spina-vulgaris	High [a]			Yes [u]

*These species are known to exhibit marked provenance response on saline soils and in some cases clones have been developed from selected individual plants. References: [a]Gill and Abrol (1991); [b]Marcar et al. (1995b); [c]Yadav and Singh (1970); [d]Jain et al. (1985); [e]Dunn et al. (1995); [f]Yadav (1989); [g]N.E. Marcar et al. unpublished data; [h]Lesueur et al. (1993); [i]Blair et al. (1988); [j]Palmer et al. (1989); [k] Ashwath et al. (1995); [l]Turnbull and de la Cruz (1991); [m]Gupta (1993); [n]Webb et al. (1984); [o]Conçalves, personal communication; [p]Duguma et al. (1994), [q]MacDicken (1994); [r]Powell (1994); [s]Halenda and Ting (1993); [t]Singh (1989); [u]Vivekanandan (1989); [v]van der Moezel et al. (1988); [w]Hussain and Gull (1993).

Responses of trees to sodic soils have generally been defined only in terms of pH, i.e. a high pH is indicative of high ESP (Gill and Abrol 1991; Hussain and Gul 1992). Response to gypsum application can also be used to determine tolerance to sodicity (Hussain et al. 1990).

No field trials are known to have been conducted specifically to establish ranking of tree species to waterlogging tolerance. This is in part due to the difficulty of establishing consistently uniform treatments and determining the degree of aeration stress. Information regarding tolerance to waterlogging or flooding in the field has usually been provided anecdotally from a variety of sources for species distribution and occurrence in particular habitats (e.g. swamps, seasonally waterlogged soils, poorly-drained soils, etc.). Often trees adapted to heavy, clay soils will be tolerant of seasonal waterlogging. Table 14.2 indicates the response of some tree species to wet and waterlogged soil.

Although physiological mechanisms have not been extensively used as screening criteria for trees, there are some prospects for including these in selection for salt tolerance. Enhanced ability to exclude Na or Cl from roots or shoots appears to be a most important mechanism operating in salt-tolerant lines of woody species. For example, Thomson (1988) found a positive correlation between Cl exclusion from the shoot and salt tolerance for clones and provenances of *Eucalyptus camaldulensis*, and a positive relationship was found between Cl exclusion from shoots and growth under salinity salt for 15 families of *Taxodium distichum* (Allen et al. 1994). Genes controlling salt tolerance mechanisms have been found in wheat and other crops but not yet in trees (Allen et al. 1994).

One potential area that warrants further investigation is the use of calorimetric measurement of dark respiration as an index of growth potential and of stress tolerance. Recent microcalorimetric experimentation at the University of California, Davis, USA, has revealed strong correlations (negative and positive depending on the variate under consideration) between several respiration-based variates determined on expanding leaves, and growth under control and stress conditions in glasshouse and field environments (Hansen et al. 1994; Anekonda et al. 1995). The decreased growth of *E. grandis* and *E. camaldulensis* seedlings with increasing salt concentrations appears to be well correlated with decreased heat loss (q) and CO_2 production (R_{CO_2}) (Table 14.3). In addition, there is some indication that the more salt-tolerant *E. camaldulensis* has relatively lower reduction in q than R_{CO_2} at 150 mol m^{-3} NaCl, compared with *E. grandis*.

Overall, it would seem that at this stage conventional tree selection and breeding provides the best chance for improvement in salt tolerance of trees (Allen et al. 1994). In order to capture useful genetically determined traits for a particular species, open-pollinated seed orchards could be established directly or by selectively thinning provenance/progeny trials. Provenance/progeny trials cum seed orchards have been recently established for *E. camaldulensis* and *Acacia ampliceps* in Pakistan (Naqvi et al. 1996). Figure 14.3 is a view of the 6-month-old *A. ampliceps* provenance/progeny trial established in Pakistan. The success of these seed orchards will depend on the degree of heritability (h^2) for survival and growth on salt-affected land as well as on site conditions that promote synchrony of flowering and good seed production. Genotypic variation for growth under salinity may be high as evidenced by high (h^2 = 0.5–0.8) narrow-sense heritabilities from glasshouse investigations of provenance/progeny variation for salt tolerance in *E. grandis* and *E. globulus* (Marcar et al. 1995a).

Table 14.3 Respiratory variables for expanding leaf tissue of one- to two-month-old, salt-treated seedlings of *Eucalyptus camaldulensis* and *Eucalyptus grandis* (mean and standard error; n =2–3 plants per treatment per species) (N.E. Marcar, unpublished data)

Species	NaCl ($mol\ m^{-3}$)	q ($\mu W\ mg^{-1}$)	R_{CO_2} ($pmol\ mg^{-1}\ s^{-1}$)	q/R_{CO_2} ($kJ\ mol^{-1}$)
Eucalyptus camaldulensis				
	0	32.6 ± 1.7	103.5 ± 28.9	279 ± 51
	75	33.4 ± 5.9	64.7 ± 8.4	516 ± 115
	150	25.6 ± 4.3	62.4 ± 18.7	445 ± 69
E. grandis				
	0	26.1 ± 1.9	59.8 ± 3.0	417 ± 36
	75	27.4 ± 0.5	53.8 ± 6.4	494 ± 72
	150	18.0 ± 3.0	29.2 ± 9.5	789 ± 194

Note: q = metabolic heat loss, R_{CO2} = the rate of CO_2 production, q/R_{CO2} =heat loss as a function of CO_2 production. For further descriptions of these parameters, refer to Hansen et al. (1994).

Figure 14.3 *Acacia ampliceps* in a provenance-progeny trial six months after planting in April 1995 on a moderately-highly saline, sodic soil near Faisalabad, Pakistan. (Photo: N.E. Marcar)

Ameliorative measures and site management

Since direct seeding on salt-affected sites is usually unreliable, planting of nursery-grown seedlings is preferred. Whilst the use of preconditioning treatments (e.g. exposure to increasing salt levels or to water-logging) in the nursery may confer advantages upon planting, no significant gains in survival and growth have been reported (e.g. Hoy et al. 1994). Preliminary results indicate that inoculation of *A. ampliceps* with salt-tolerant *Rhizobium* increases seedling growth in the field (Zou 1995) as well as in the glasshouse (Marcar et al. 1991a; Zou et al. 1995).

Land preparation techniques and cultural operations that have shown significant improvements in tree performance, particularly on survival, include:

(i) Mechanical ripping of soil with tynes to break up plough hardpans, clay layers or calcium carbonate hardpans (kankar layers), or manual digging or mechanical augering of planting holes (Gill and Abrol 1991). The soil replaced in the hole may be chemically amended with gypsum and fertilizers (Grewal and Abrol 1986). Caution should be exercised with auger holes since smooth walls may increase soil strength and make it difficult for tree roots to penetrate the walls and spread laterally (Chaturvedi 1985).

(ii) Use of saucer pits and furrows as water harvesting techniques. In this method seedlings are planted in a depression designed to collect rainfall. The technique is appropriate in drought-prone and/or saline soils without a high watertable.

(iii) Use of mounds in areas affected by waterlogging to give seedlings access to a volume of aerated soil above the watertable. The trench-ridge technique (Yadav 1989) is widely used in Pakistan and India and the double ridge mound has been very effective in aiding shrub and tree growth, though not necessarily survival (Hoy et al. 1994). In the double-ridge mound method, the trough between the ridges, where seedlings are planted, collects rain which leaches salt from the soil below the trough, i.e. the seedling root zone (Marcar et al. 1995b). These mounds can be manually, or preferably, mechanically constructed (Malcolm and Allen 1981).

(iv) Provision of subsurface drainage. This can be provided either by vertical drainage (e.g. pumping from tube wells) or horizontal drainage (e.g. deep open ditches (trenches), slotted pipe (tile or plastic) drains and mole drains) or both, to remove excess water.

(v) Application of mulches to reduce evaporation (drying of the surface soils) and accumulation of salt at and near the soil surface. Mulches include straw, cotton burrs, vermiculite, peat, sand and polythene. Figure 14.4 illustrates significant improvement in survival and growth of 19-month-old *A. ampliceps* on a moderately saline, nutritionally-poor site in northeastern Thailand using mulch in combination with other treatments (for earlier reference to this trial refer to Marcar et al. 1991b). Mulch application had the major beneficial effect on survival, probably through reducing surface soil salinities, but gypsum and fertilizer application had a greater effect on growth, probably related to better root growth due to improved soil structure and nutrient supply. The effects of these treatments have tended to decline after several years.

(vi) Addition of organic and inorganic fertilizers. Sodic soils are often deficient in organic matter, nitrogen, zinc and other nutrients. Gypsum can be mixed in with sodic soil to replace excess Na with Ca, but this will only be successful if sufficient water is provided to leach excess Na beyond the root-zone. Significant survival and growth advantages accrue from use of farmyard manure in addition to gypsum with sodic soils, either mixed with original soil in auger holes (Grewal and Abrol 1986), or broadcast onto the soil (Singh et al. 1989), and lead to more efficient use of fertilizers by reducing soil pH. Figure 14.5 depicts the marked growth response of *E. camaldulensis* to addition of combined N, P and gypsum on a moderately saline-sodic site near Lahore, Pakistan (N. Marcar, unpublished data).

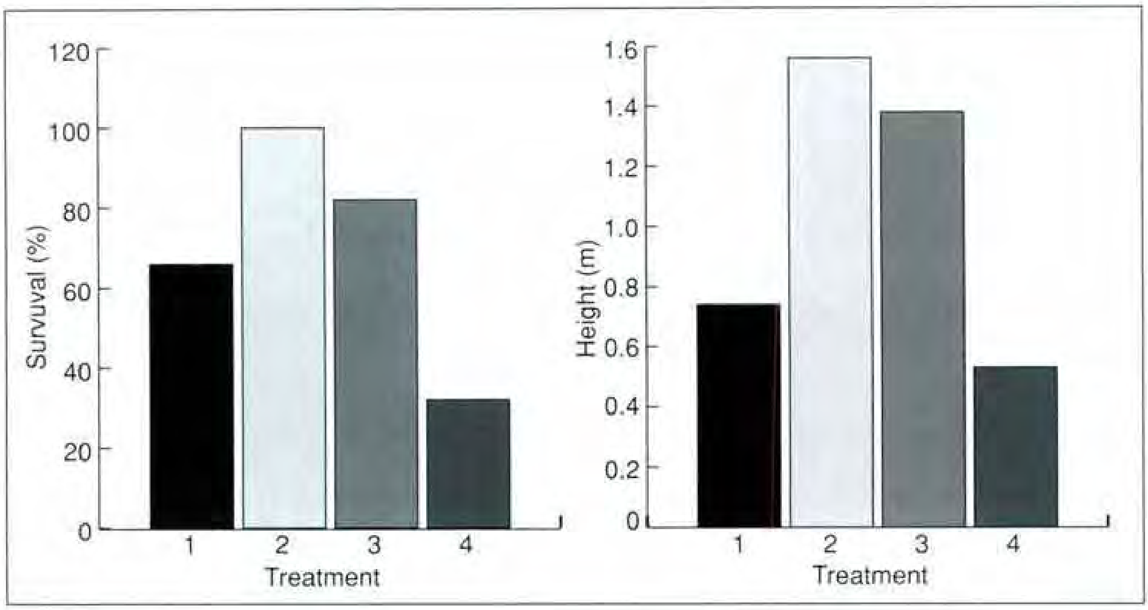

Figure 14.4 Mean survival and height of 19-month-old *Acacia ampliceps* in response to mulch application in combination with other treatments. These unpublished data are selected from a wider range of treatments imposed in an establishment technique trial near Khorat, NE Thailand (Marcar et al. 1991). Treatment 1 = M; treatment 2 = M + G + FM; treatment 3 = M + G + NP; treatment 4 = control. M = rice hulls mulch; G = gypsum (2 kg per tree); FM = farmyard manure (3 kg per tree) and NP = nitrogen/phosphorus fertilizer (15 g per tree).

Figure 14.5 Two-yr-old *Eucalyptus camaldulensis* on a moderately saline, sodic soil near Lahore, Pakistan illustrating response to a combined application of N, P and gypsum. The block of trees at the front left is a control (no fertilizer or gypsum), whereas the block at the front right has received 1 kg urea, 200 g diammonium phosphate and 1kg gypsum per tree. (Photo: N.E. Marcar)

Reforestation options

Reforestation offers prospects of both utilising and ameliorating salt-affected land. The most appropriate form of reforestation of salt-affected land in many countries is for social and farm forestry through involvement of landholders, agencies and private companies (Gill and Abrol 1991). Salt-affected areas are often sparsely populated and living standards are often lower than in other areas of the region (Vivekanandan 1989). By far the major impetus for tree planting in developing countries is to produce firewood for domestic consumption (Midgley et al. 1986), and utilisation of these lands will reduce the depletion of available forest resources and avoid the need to grow tree crops on more fertile land that could be used for other crops.

However, there is also scope for establishing commercial-scale wood-producing plantations on slightly to moderately salt-affected land (Marcar and Crawford 1996). In southeastern Australia, there is currently considerable interest in growing commercial eucalypts (e.g. *E. grandis, E. globulus*) in irrigation areas much of which are underlain with shallow, saline water tables. Other options, such as development of eucalypt plantations for industrial and pharmaceutical oil production in the wheat belt of Western Australia, are being pursued on both saline and nonsaline land (Bartle 1994). In Western Australia, there is also a large government-sponsored program under way to plant *E. globulus* on farms located on nonsaline, recharge areas in dryland, salt-affected catchments to provide a pulpwood resource and control the spread of rising groundwater (Bartle 1991).

If good quality irrigation water is available, the prospect of good tree growth on saline land is much better. For example, in trials at Faisalabad (Pakistan), *E. camaldulensis* has grown in height at 2–3 m per yr on a saline-sodic soil of moderate salinity ($EC_e < 10$ dS m^{-1}) and furrow-irrigated with good quality water (R. Qureshi and M. Ahmed, pers. comm.). Mean annual increments (MAIs) for volume of wood of ca. 10–15 m^3 ha^{-1} yr^{-1} are possible for 5–7-yr rotations of *E. camaldulensis* at a density of ca. 1000 trees ha^{-1} under such conditions. Success has been attributed to significant leaching of salts beyond the root zone.

However, if watertables are close to the surface (e.g. within 1 m for clay soils), only very limited leaching is possible and yields will be lower. Thus good irrigation management, coupled with correct species choice and addition of suitable amendments (e.g. gypsum), may enable farmers to consider tree products other than firewood in their whole-farm plans. Short-rotation tree crops for pulpwood may compete favourably with annual crop production systems and use considerably less water, since within one year trees could access groundwater as well as stored soil moisture derived from rainfall.

Potential for land rehabilitation

Benefits of two main types may be provided by trees planted within areas that are salt-affected and/or have saline water tables at shallow depth. These are: i) lowering of saline watertables, through either control of accessions to or withdrawal from groundwater, thereby improving agricultural productivity; and ii) use of saline groundwater which would otherwise have flowed to streams and eventually rivers, by subsurface seepage or deliberate drainage disposal, thereby reducing environmental damage. Trees planted alongside irrigation channels may also help keep watertables down by intercepting seepage. This is particularly important in areas where canals and channels are mainly unlined.

Water use per unit land area is an important determinant of the capacity of trees to lower watertables. Water use per unit land area will be the product of individual tree water use and density of planting (Greenwood et al. 1994). Individual tree water use is closely linked with stem or sapwood cross-sectional area (Chapter 6). Two methods are currently used to determine single-tree water use: sap flow velocity (Hatton et al. 1990) and deuterium tracing (Calder 1994). Fast-growing trees, such as *E. camaldulensis*, are likely to have high annual water use, because of: i) their high leaf area indices (L^*) and evergreen habit; ii) their extensive and deep root systems; and iii) their relative immunity to changes in the dryness of the atmosphere measured as vapour pressure deficit (VPD).

Preliminary data from studies on a moderately saline site near Lahore (Pakistan) indicate water use of up to 1300 mm per year (ca. 2.5 × annual average rainfall, supplemented by irrigation) for winter-irrigated *E. camaldulensis* and *E. microtheca* (J. Morris, unpublished data). Many species will probably use water from watertables with EC up to 10 dS m^{-1} without marked reduction in transpiration rate, but tree water use per unit land area will be significantly lowered as canopy area and sapwood area (or the approximate surrogate measure of breast height diameter) are decreased due to salinity. However, the proportion of groundwater directly used by trees has been measured in only a few studies, particularly using isotopic means (e.g. Thorburn et al. 1993). With such knowledge it will be possible to determine threshold salinities, i.e. those salinities at which particular species can no longer transpire water (Thorburn 1996).

Differences between species may also be rather smaller than those due to climatic factors (e.g. humidity) and leaf area index. Few systematic comparisons of water use between provenances of particular tree species have been made so far. Preliminary data from a study of twelve *E. camaldulensis* provenances on a saline discharge area have shown little evidence of differences in water use determined by the heat-pulse technique per unit of sapwood area (J. Morris, unpublished data).

There are several examples of significant lowering of saline watertables under and/or near to plantations and agroforests. In Australia, the best examples are from dryland sites in Western Australia (Schofield et al. 1989; George 1990; Greenwood et al. 1994) and in Victoria (Morris 1991), and from irrigated sites in Victoria (2 m watertable lowering for an 8-yr-old eucalypt plantation; Heupermann 1995). The effectiveness of plantations will be related to tree density, the proportion of the area planted, crown cover, root architecture, soil hydraulic characteristics and groundwater dynamics. One example of successful lowering of an elevated watertable is an alley farming trial near Boundain, Western Australia (Schofield et al. 1989; Scott and Crossley 1996). Figure 14.6 presents data over the period 1981–1994 from the Boundain site (Scott and Crossley 1996). At this site several salt-tolerant eucalypts, including *E. occidentalis*, were planted as single rows with alley spacings of 25 and 12.5 m, to provide tree densities of about 80 and 160 stems ha^{-1}. Trees have lowered the watertable by about 12 m relative to annual pasture. There is some suggestion that the control over watertable rise by tree plantations may be effective only in the short to medium term, because of the potential for salts to increase in the root-zone.

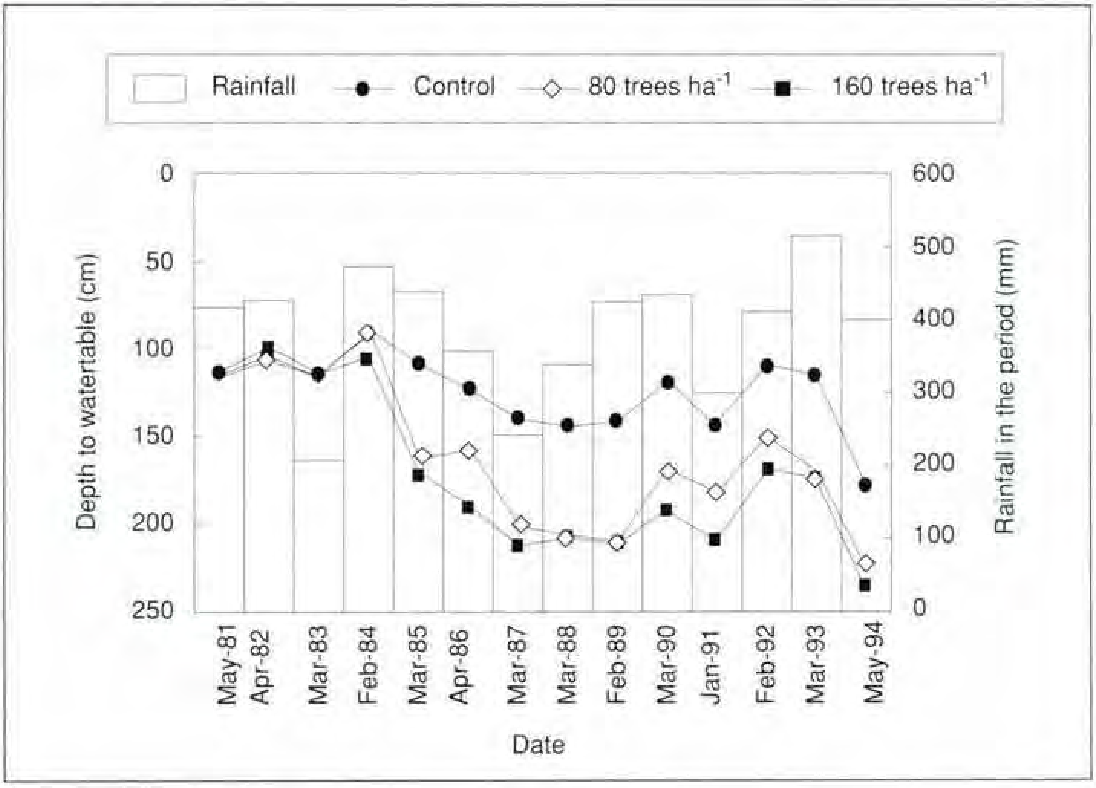

Figure 14.6 Groundwater level variation on a saline site underlain by a shallow, highly saline watertable at Boundain, Western Australia, in response to agroforestry plantings of salt-tolerant eucalypts planted at the equivalent of 80 and 160 trees per ha, relative to pasture, and rainfall (Scott and Crossley 1996). Data show annual minimum levels of groundwater (in summer) over time. Rainfall for the measurement periods is represented as bars. Figure reproduced with permission of the authors

There are few published data for changes in groundwater and soil salinity as a consequence of groundwater lowering. The long-term consequences for salt distribution under trees planted on saline land (dryland or irrigated) or on nonsaline land where tree roots have access to saline groundwater are by no means certain. Such information is vital to prediction of long-term tree survival, growth and water use. Depending on soil properties (e.g. clay content), active rooting depth, lateral and vertical groundwater flow, salt diffusion in the saturated zone and the degree of leaching possible, it is expected that salt will accumulate somewhere in the soil-groundwater system. This is because salt exclusion by roots is the principal feature associated with salt tolerance for most tree species. Although soil and groundwater salinity beneath eucalypt plantations established over a shallow saline watertables has been shown to increase in different parts of the root-zone (Heupermann 1995; Stolte et al. 1996), other studies have suggested that salt concentrations have not continued to increase because of leaching from watertable fluctuations and seasonal and episodic rainfall events (Morris 1991; Thorburn 1996).

Reuse of shallow groundwater (pumped via tubewells or bores) or saline drainage water for tree production systems will provide an increasing challenge for foresters and agroforesters. These systems are generally better targeted to sandy/loamy textured soils because of the danger associated with excessive salt accumulation in clay-dominated soils. Pilot studies have been established near Hyderabad in Pakistan, in the San Joaquin Valley of California (Tangi and Karajeh 1993) and in Victoria, Australia (Heath and Heupermann 1994). In the latter two cases, agroforestry systems are being tested to determine the feasibility of reducing the volume of saline drainage water for ultimate disposal. The success of these plantations will be dependent on how well salt concentrations in the root-zone can be managed and on the salt tolerance of the species grown. The major constraint in using poor quality water will be the concentration of sodium carbonate, salt and nutrients.

If leaching fractions are relatively high, soils are permeable and watertables are deep, the potential for salt accumulation will be relatively small (e.g. in a woodlot on loamy sand in Loxton Irrigation Area, South Australia (Sweeney and Frahn 1992)). If however watertables are high, drainage is limited and soils are less permeable, salt accumulation at the top of the capillary fringe (phreatic surface) can be very high (e.g. a woodlot on a clay soil at Kyabram, Victoria (A. Heupermann, pers. comm.)). Evidence from limited studies of tree plantations on or near dryland discharge seeps suggests that salt build-up in or below the root zone is much less than expected from simple models based on annual salt input and annual evapotranspiration (Schofield and Bari 1991).

Sodic soils may be ameliorated by activity of plant roots and soil microorganisms. The production of carbonic and other acids resulting from root respiration and organic matter decomposition can liberate appreciable quantities of soluble Ca from insoluble $CaCO_3$, allowing for continued exchange of Na with Ca. Coupled with adequate leaching, using low-Na irrigation water and/or monsoonal rain, much of the Na can be removed from the root-zone. Successful examples of this process include plantings of *Leptochloa fusca* (kallar grass) (Mahmood et al. 1994), *Acacia nilotica* (Gill et al. 1987) and agroforestry plantings of *Prosopis juliflora* and *L. fusca* (Singh 1995). Gill et al. (1987) found significant reductions in soil pH and EC for both *A. nilotica* and *Eucalyptus tereticornis* but greater increase in organic carbon under *A. nilotica*. Farmers in the Sindh province of Pakistan have known for a long time that saline-sodic soils can be improved by planting closely-spaced, short rotations of *A. nilotica*, in a management system called hurries, prior to cropping; Keerio (1993) has documented some physical and chemical changes related to this improvement.

Reforestation of Acid Soils

Approximately 3950 M ha or 30% of the worlds land area is composed of acid soils, where acid soils are considered to be those with pH_{H_2O} less than 5.5 (von Uexkull and Mutert 1995). According to Oldeman et al. (1991) only a small area (5.7 M ha) has become acidified due to human causes. In the humid tropics, acid soils are relatively more important in Latin America (81% of the land area), but significant areas are also present in Africa (56%) and Asia (38%) (Sanchez 1987). Southeast Asia and the Pacific (excluding Australia and New Zealand) have 315 M ha of acid soils, South America 676 M ha and Africa 659 M ha (von Uexkull and Mutert 1995). Most acid soils in tropical Asia are classified as Ultisols, with fewer Oxisols and perhaps a few Alfisols (von Uexkull and Bosshart 1989), whereas in tropical America or tropical Africa, Oxisols dominate (Sanchez 1987). Physical and chemical properties of Oxisols and Ultisols are discussed in Chapter 4.

Until the turn of the century, vast areas of tropical acid soils remained largely untouched as primary forest, with only a small number of people practicing shifting cultivation. Currently, more than 11 M ha of tropical acid soils are cleared annually, mostly from primary forest, and converted to agriculture and, to a lesser extent, forest plantations (von Uexkull and Mutert 1995). These practices lead to nutrient loss and often to the development of savanna and shrubland with acid, infertile soils. For example, an estimated 20 M ha of *Imperata cylindrica* (alang alang) grasslands have developed in Southeast Asia alone. Similar grasslands have also developed in the Pacific and Africa which have highly acid, infertile soils with generally poor structure and small amounts of organic matter. Tree growing has the potential to provide a successful timber-based local industry in *Imperata*-infested areas; but appropriate technological (fertilizer, herbicide and soil cultivation) and socioeconomic (land tenure and ownership) efforts would be required (Turvey 1994) for sustained production.

Characterisation of and processes in acid soils

Acidification of a soil refers to processes that increase protons and acid-cations with an accompanying decrease in base cations, primarily of the exchange complex. It is also associated with a decrease in soil pH. Any change in soil pH depends upon the nature and capacity of the buffering systems in a soil. Therefore soil pH is the direct outcome of the buffering nature of a soil and is considered to be a prime determinant of most chemical and biological properties of soils. Based on the stability of soil minerals and oxides, Ulrich (1981) outlined six possible buffer ranges in soils of the temperate region; these are expected to be valid for tropical and subtropical areas:

Buffer range	**pH**
i. Calcium carbonate	>8 to 6.2
ii. Silicate[a]	6.2 to 5.0
iii. Cation-exchange	5.0 to 4.2
iv. Aluminium	4.2 to 3.8
v. Aluminium/iron	3.8 to 3.2
vi. Iron	3.2 to 2.4

[a] Silicate weathering can occur at other pH values as well

The soil pH values referred to here correspond to those measured in an equilibrium soil solution or in a soil/water suspension (usually a saturation paste). On addition of a salt ($CaCl_2$ or KCl) to the soil/water suspension, the pH drops to values corresponding to the buffer range which is attained by high proton or salt loads (e.g. following fertilisation). For describing acid soils, measurement of exchangeable cations by using unbuffered salt solutions (e.g. NH_4Cl or $BaCl_2$) is recommended, because any change in the pH of the salt solution can be used to calculate exchangeable H-ions after accounting for those obtained from dissociation of Al^{3+}. For determination of exchange sites, adjustment of ionic strength of the solution and the compulsive exchange method as proposed by Gillman (1979) are recommended.

Nutritional factors including metal toxicities which limit plant biomass production vary for soils belonging to each of the above buffer ranges. For example, nutritional limitations for trees in the calcium carbonate buffer range will be: a) unfavourable cation uptake due to excessive amounts of Ca (mostly causing K deficiency due to low K:Ca ratio); b) limited solubility of metallic trace elements causing deficiencies of Mn, Fe, Cu and Zn; and c) an unbalanced NH_4 and NO_3 ratio for N uptake. Deficiencies in N and P may become important in soils belonging to ranges (iii) to (v) because large amounts of metals may decrease biotic activity and organic matter turnover resulting in the retention of N, P and base cations by organic biomass. Metal toxicities may be acute in (iv) to (vi) ranges and may directly affect plant growth, especially if organic matter content of the soil is low, e.g. as might occur during plantation establishment (for discussion refer to Khanna and Ulrich 1991). Ca, Mg and P are expected to be deficient in this range. Most acid soils in the tropics and subtropics should lie in the ranges of (iii) to (v), except for the special case of acid sulfate soils. Acid sulfate soils are formed by the oxidation of pyrite, FeS_2, which is a common and stable constituent of marine sediments. Under waterlogged conditions and in the anaerobic state, potential acid sulfate soils are usually near-neutral, but draining these soils for agriculture allows air to penetrate the soil so that the pyrite oxidises to form sulfuric acid, and unless the soil happens to be calcareous the pH rapidly decreases to 3.0 or less (Bloomfield and Zahari 1982).

Acidity is produced both by natural processes and by those associated with land (e.g. agriculture, forest) management. For example, removal of base cations during biomass harvesting and the accelerated leaching of base cations following site preparation will contribute in a significant way to soil acidification (Chapter 10). Knoepp and Swank (1994) reported a significant decrease in base cations and pH in surface soils during a 20-yr period of two aggrading stands of mixed hardwood and *Pinus strobus* L. in western North Carolina (USA) which they attributed to leaching and to the sequestration of bases in biomass.

A number of ecosystem processes contribute to proton sources either as inputs from external sources (refer to Rodhe and Herrera (1988) for details on atmospheric depositions in tropics) or as a result of uncoupled fluxes of C and nutrients within a system, i.e. internal proton sources (for a discussion on acidification and deacidification processes in plantation forests refer to Khanna and Ulrich 1984). Major processes are: i) mineralisation of organic matter and leaching of HCO_3^- and H_2CO_3 (plant and microbial respiration) and the accompanying losses of bases, ii) nitrogen transformations, uptake and leaching (mostly of NO_3^-); iii) accumulation of organic matter as aboveground biomass, humus layer and soil organic matter; iv) leaching of organic anions, especially during the periods of biomass aggradation; and v) acid deposition of H_2SO_4, HNO_3 and $(NH_4)_2SO_4$.

All well-leached soils (uncoupled systems) tend to become acid in time; the rate of change will, however, depend upon the rate at which the protons are added (fertilisation, atmospheric inputs) or produced (mineralisation, cation uptake) and the nature and rate of proton buffering (described above). Both will vary temporally and spatially (depthwise) (Chapter 10).

During deforestation, a significant amount of bases is removed from the site in harvested biomass. Vegetation components vary in their content of bases, for example, bark of some eucalypts is rich in Ca (Turner and Lambert 1986), and the removal or retention of those components will affect the balance of bases on a site accordingly. Removal of vegetation may change the microclimate and hydrological cycle on a site, resulting in increased mineralisation of organic matter and accelerated soil erosion and leaching, which can cause depletion of bases and nutrients and an increase in soil acidity. Slash-and-burn activity will deplete forest sites of significant amounts of nitrogen, phosphorus, sulfur and base cations and may enhance erosion of surface soil and ash by reducing the vegetative cover. These activities can further intensify acidification. The potential usefulness of bases added in ash will depend upon the subsequent site preparation practices such as mixing ash with soil (cultivation) which will result in higher solubility of ash. Heaping of slash (and parts of surface soil) may cause two important changes in soils: a) relatively higher mineralisation of soil organic matter and N on and around the windrows, and an excessive amount of mineral N which may be lost together with bases resulting in positive proton balance and losses of base cations; and b) additional heterogeneity in surface soil especially relating to exchange capacity and exchangeable bases. Burning and heaping of slash are thus two severe treatments which, if possible, are best avoided.

Uncomplexed (by organic matter) and monomer forms of Al, also called free Al, are considered toxic to plant growth by affecting functioning and growth of roots either directly or indirectly through interference in the development and functioning of symbiotic associations with rhizobia, mycorrhizas and actinomycetes. Many tree species in tropical forests have developed strategies which are physiologically-based, to deal with high Al^{3+} in soils (Sanhuenza et al. 1988). For a detailed discussion on mechanisms of tolerance and avoidance of acidity (high levels of Al and Mn) by trees, refer to the review paper by Fisher and Juo (1995).

A further constraint to plant growth in highly acid soils may arise from water stress (Table 14.1) which results from the restriction of root growth (root length and root hairs) into deeper soil horizons where the B horizon has been acidified, often as a direct result of Al toxicity (Adams 1984). Plants adapt by increasing their root density in surface soil, but this may further accentuate water stress problem when surface soil dries out, especially in seasonally dry periods. Other factors affecting plant growth on acid soils include deficiency of P, B and Mo. Deficiency of P has a number of implications including its effects on biological fixation of N, which can be significantly reduced in soils with highly acid, low P characteristics.

For the five agroecological regions of the tropics (humid tropics, acid savannas, semi-arid tropics, tropical steeplands and tropical wetlands), Sanchez and Logan (1992) observed that Al-toxicity, acidity without Al-toxicity and high P-fixation by Fe-oxides are the major soil constraints to productivity; additionally in the humid tropics and acid savannas low reserves of soil nutrients are a major constraint.

Use of acid soils for plantations and ameliorative measures

Acid soils can be used for fast-growing plantations in the tropics, but to achieve sustained high productivity a number of soil and plant-based management practices may be required:

Tree evaluation, selection and improvement

Evaluation and selection of tree species for acid soils should consider their physiological characteristics. Those traits should allow plants to avoid or tolerate high levels of soil Al and Mn, to have relatively low requirements of P or to acquire sufficient P to sustain high growth rates, and to acquire symbionts to fix nitrogen under acid conditions. According to Marschner (1995), avoidance mechanisms are more common for adaptation of plants to acid soils. Examples of such mechanisms are: i) root-induced changes in the rhizosphere such as pH increase; ii) release of chelators for Al, higher activity of ectoenzymes (acid phosphatases); and iii) increase in root surface area via mycorrhizae.

Studies which compare the performance of tree species and their symbionts (rhizobia and VA or ectomycorrhiza) are often undertaken by growing seedlings in pots containing acid (or reconstituted acid) soils (Turnbull and de la Cruz 1991; Ashwath et al. 1995). The acid soils are sometimes amended (e.g. with lime or with a potentially limiting nutrient such as N or P) to provide information on potential growth for comparison under nonlimiting situations. Soil cultures have also been used to separate the individual effects of amending pH thereby reducing Al^{3+} concentrations (via liming) and enhanced Ca supply using Oxisols and Ultisols (e.g. for *Leucaena leucocephala*, Blair et al. 1988). Growth of particular species on different soils with similar pH may differ markedly. Ashwath et al. (1995) found large differences in growth and nodulation response of 20 subtropical and tropical *Acacia* species when grown on two acid soils.

The activity of Al^{3+} in soil solution is a good indicator of root growth of crop plants (Foy 1984; Bruce et al. 1988) and critical values of ca. 4 M Al^{3+} have been proposed. Ca deficiency and Al toxicity are closely linked (because of their antagonistic effects on permeability and elasticity of membranes in the plant) and the ratio of Ca^{2+}:Al^{3+} in soil solution can therefore be used to assess the risk of Al toxicity and observed symptoms in tree roots (Rost-Siebert 1985). Solution cultures are sometimes used to define the effects of Al^{3+} concentrations on morphology of roots, but their use for determining species and within-species differences due to Al concentrations (e.g. *Robinia pseudoacacia* (black locust), Oakes and Foy 1984) are questionable, because decrease in root activity due to Al may not affect the uptake of water and nutrients when these are supplied in higher concentrations in solution cultures. The potential of the root to regenerate after it is subjected to high levels of

Al has been proposed as a useful index with which to screen plants (e.g. loblolly pine, Paganelli et al. 1987).

Some plantation species are well adapted to acid soils. *Eucalyptus grandis* appears to grow very well on acid soils in Brazil (J.L.M. Gonçalves, pers. comm.) probably because of its capacity to vary Ca levels in the tissue (data given in Chapter 10). *Acacia auriculiformis*, *Acacia aulacocarpa*, *Acacia crassicarpa* and *Acacia mangium* have grown very well on highly acid (pH 3.5–4.5) soils on Hainan Island, China (Anon. 1992), and *Acacia cincinnata*, *Acacia crassicarpa* and *Acacia mangium* were recommended for planting on infertile acid soils of Hawaii (Cole et al. 1996). Table 14.2 lists species tolerant to slight, moderate or severe soil acidity.

Low pH generally inhibits nitrogen fixation by reducing the development of rhizobia, increasing the numbers of ineffective rhizobia or disrupting the infection process (Sprent and Sprent 1990). In general, the critical pH for nodulation of most legumes is above pH 4.5 to 5.5 (Dixon and Wheeler 1983). Ahmad and Ng (1981) reported that growth of *Leucaena leucocephala* decreased 5-fold from pH 4.9 to 4.4 and this was associated with a 3-fold decrease in the amount of *Rhizobium* in the soil. In southern Vietnam, *A. auriculiformis* grown in acid sulfate soils of pH less than 4.0 nodulated profusely in the undecomposed litter layer but not in the highly acid mineral soil (MacDicken 1994); this observation may be related to increased Al-organic ion complexes in leaf litter. Results of soil sampling from 26 *A. auriculiformis* plantations showed that root nodulation was not affected by pHs as low as 4.5 (Sankaran et al. 1993).

Acid-tolerant *Rhizobium* for *A. mangium* and *A. auriculiformis* has been selected (Dart et al. 1991). In their study on nodulation of different acacia species, Ashwath et al. (1995) reported that size and number of nodules were strongly influenced by water stress and soil acidity. As is the case with salinity, improvement of acidity tolerance of *Rhizobium* is likely to be an important research goal only when the host plant is also able to grow well under acid conditions. In a recent review on nitrogen-fixing trees and shrubs for acid soil, Powell (1995) has suggested a number of *Acacia* spp., *Casuarina* spp. and *Inga* spp., and *Gliricidia sepium* as useful trees for acid soils.

Whilst considerable efforts have been made to improve the acidity tolerance of *Leucaena*, and in particular *L. leucocephala*, especially through hybridisation programs using soil-grown plants in glasshouse and field environments (Hutton and Sousa 1985), no such program has been initiated for plantation-grown tree species. Also, no program specifically aimed at selection for Al-tolerance has been initiated in woody plants, although heritability of Al-tolerance has been demonstrated in a few species including *Populus* (Schaedel et al. 1989). Mechanisms conferring increased tolerance may be external to the root (e.g. secretion of organic acids and other compounds), within the root (e.g. membrane transport or protection of crucial metabolic processes) or at the leaf level (e.g. immobilisation of Al). Aluminium can reduce Ca uptake by competing for or blocking Ca binding sites on root surfaces. Aluminium can also accumulate in cell walls and react with calcium pectate to affect cation exchange capacity of roots and therefore, potentially, water and nutrient uptake (Blamey et al. 1993). Some tropical tree species are able to accumulate very high foliar Al concentrations with no obvious symptoms (Sanhuenza et al. 1988).

Ameliorative measures and site management

Various site parameters which can be used to describe soil acidification have been given by Meiwes et al. (1986). They include: i) soil pH (pH in saturation extract or soil water and in dilute salt solutions); ii) exchangeable cation concentrations; iii) % Al saturation; iv) the ratio between base and acid cations in the humus layers; and v) Ca to Al ratios in soil solutions and fine roots. Some assessment of N dynamics and P supply in soils is very important. Information on these soil characteristics will assist in defining the most suitable management practice for an acid soil site including possible ameliorative measures:

(i) Application of lime and ash materials: Chemical amelioration of acid soils is still the only way to ensure sufficient rise in pH for satisfactory tree growth. The amount of lime ($CaCO_3$) required depends on the initial pH and buffer capacity of soils (e.g. Aitken et al. 1990). However, application of lime is usually expensive and may be unaffordable in many forestry plantations or agroforestry systems. Moreover, solubility of lime is low depending mainly upon proton inputs. Under an environment of low proton inputs, most of the lime may be retained in the surface few centimetres of soil. Mixing of lime with the soil is therefore very important to gain any benefit from liming. In order to ameliorate soil acidity at greater depths, application of lime and gypsum ($CaSO_4$) is recommended. Recent work with *Leucaena* suggests that where Ca levels are low and where amelioration at depth is preferred, $CaSO_4$ should be applied (Blair et al. 1988).

Wherever wood ash becomes available, for example after burning of harvested wood (or bark) for energy production, it should be mixed with the surface soil. Base cations in ash have varying solubility and some, like K, are highly soluble whereas the solubility of others, like Ca and P, depends upon the availability of protons, as is the case with liming materials (Khanna et al. 1994).

In addition to the changes in chemical processes in soils, inputs of both liming and ash materials will initiate or enhance many biological processes in soils such as organic matter decomposition, mineralisation and nitrification of N and P and faunal population and activity. Timing, rate and method of application of liming and ash materials will therefore become an important factor in obtaining the best results. In most cases, dolomite liming materials should be preferred.

(ii) Managing base cation supply in acid soil: Plantation tree species vary in the total amount of bases which they accumulate (Chapters 10 and 11). Moreover some plant components such as bark have greater amounts of bases than others. Therefore management options should consider: a) avoiding the planting of high base-accumulating species; b) leaving bark well distributed on the site; and c) avoiding slash fire completely, or restricting it to only special situations.

(iii) Organic matter additions: Addition of organic matter reduces free Al in the soil by two processes: a) organic acids produced during decomposition processes can complex Al and turn it into a nontoxic form. Greater amounts of organic acids have been reported in forest soils than in cultivated agricultural soils (Hue et. al. 1986); this is considered to be related to higher microbial activity in forest soils. Al-detoxifying capacities of organic acids depends upon the amount and type of the carboxylic acid (relative position of OH/COOH groups on their main C chain, Hue et. al. 1986) and the possibility of reaction of organic acids with free Al. b) inputs of cations with organic matter additions. The base composition of plant residues can vary and the application of, for example, base-rich plant residues when added as prunings will decrease Al toxicity in a significant way as shown in Table 14.4 (Wong and Nortcliff 1995). Of the three plant residues tested, those of *Leucaena diversifolia* contained the largest amount of bases and caused greatest reduction in exchangeable Al in an Oxisol. *Leucaena* residues exhibited high decomposition rates and rapid transfer of the bases to soils because they contained relatively small amounts of lignin and had a better C:N ratio. Many of the experiments in the past have overlooked this role of releasing base cations when organic matter was added as pruning or mulches. Increases in exchangeable Al over time were correlated with decreases in soil pH.

Table 14.4 Composition of plant residues from *Grevillea robusta*, *Calliandra calothyrisus* and *Leucaena diversifolia* and their effect on exchangeable Al of an Oxisol from Burundi when 4.5 g of residues were incubated with 145.5 g of soil (3% by weight). Data extracted from Wong and Nortcliff (1995).

Species	**Residue**						**Exchangeable Al ($\mathrm{mmol_c\ kg^{-1}}$) after incubation**	
	K	**Ca + Mg**	**Sum**	**C:N**	**Polyphenol**	**Lignin**	**14 days**[a]	**98 days**[a]
		($\mathrm{mol_c\ kg^{-1}}$)			**(%)**			
Grevillea	0.37	0.57	0.94	27	1.84	16.7	7.6	7.8
Calliandra	0.24	1.01	1.25	15	2.39	4.30	3.9	9.7
Leucaena	0.32	1.93	2.25	16	1.68	3.10	0	3.9

[a] Before incubation with residues the soil had 18 $\mathrm{mmol_c\ kg^{-1}}$ of exchangeable Al

(iv) Better control of N dynamics: Processes of nitrogen mineralisation, uptake and leaching in soils affect the proton balance in a significant way. Options leading to a decrease in the leaching of nitrates, for example, through management of vegetation (weeds) or by promoting uptake of excessive N by deep-rooted species in mixed stands, may be useful in decreasing further losses of bases from soils especially during site conversion and early phases of plantation growth. Delaying the application of N fertilizer (increasing the efficiency of N fertilizer) and use of mixed species to avoid excessive N build-up by N-fixing trees, may be other management strategies worthy of consideration.

Reforestation options

Both plantation and agroforestry systems may be used for tree growing on acidic land. Several tree species, for example *Eucalyptus grandis* × *E. urophylla* hybrid and *Acacia mangium*, have grown very well (11–12 m and 40–45 m^3 ha^{-1} in 2.5 yr) on acid soils in China (Menz and Lawrence 1995). Herbicide and fertilizer (N and P) application are essential to achieve high productivity. In Brazil, eucalypt plantations on highly acidic, infertile savanna soils are managed with applications of NPK, rock phosphate and (where there is a prolonged dry season) boron fertilizers (Barros et al. 1991). Application of organic fertilizers to l2-month-old *E. grandis* on an acid (pH_{KCl} 4.0), low organic carbon (< 0.3%) soil on the Zululand Coastal Plain (South Africa) resulted in up to 73% height growth increase (Noble et al. 1991). Cole et al. (1996) recommended *A. cincinnata*, *A. crassicarpa* and *A. mangium* for planting on acid soils of low fertility in Hawaii. Under high fertility conditions which included 8 t ha^{-1} lime and high rates of NPK applications, eight of the twelve acacia species tested showed faster growth; the native Hawaiian species *Acacia koa* had a ten-fold increase in stem volume.

Sufficient information is available to develop technologies which can be used to successfully establish plantations on grasslands dominated by *Imperata cylindrica*. But most of these require high resource inputs (several ploughing and harrowing operations, heavy frequent doses of weedicide and fertilizer application) which in many instances may not be an economically feasible option. In an experiment on establishment and early growth of a number of tree species on imperata grasslands in South Kalimantan, Otsamo (1995) observed that the application of phosphorus (if possible NPK-fertilizer) is essential to speed up early tree growth to gain control over the grass. Among fast growing trees *A. mangium* showed encouraging performance.

The occurrence of acid sulfate soils is usually sporadic, spatially and within a profile. Collectively the area of potential and actual acid sulfate soils in the tropics is ca. 15 M ha (Bloomfield and Zahari 1982). Mixed forestry/rice cultivation can potentially support a sustainable land-use system on some 1.5 M ha of acid sulfate soils prone to seasonal inundation in the Mekong Delta of Vietnam (S.J. Midgley pers. comm.). The use of *Melaleuca* is particularly attractive because of the variety of tree products obtained from the forest and lower establishment costs compared to *Eucalyptus*, because there is no need to create mounds. In a species and provenance trial in the Mekong Delta, southern Vietnam, *Melaleuca leucadendra* from Australia showed better survival and growth during 18 months after planting than the local species *(Melaleuca cajuputi)* (J.C. Doran pers. comm.). In addition to melaleucas, *A. mangium* and *E. tereticornis* (particularly provenances from waterlogged areas of Papua New Guinea and north Queensland) are showing promise (J.C. Doran, J. Simpson and S.J. Midgley pers. comm.).

Potential for land rehabilitation

There is some evidence on the potential role of trees for preventing soil acidification, especially if they produce litter rich in bases. For example, litter and detritus from *Gmelina arborea* contain twice as much Ca as those of virgin forest trees or mature pine plantations, while the Mg content of litter was three times as high as in *Pinus* litter (Sanchez et al. 1985). Dhyani and Singh (1995) claim that accumulation of large amounts of soluble cations under stands of trees grown on extremely P-deficient acid Alfilsols in northeastern India suppressed exchangeable Al. But the role of trees in ameliorating acidity can only be considered in cases where they can accumulate nitrates or bases from deeper horizons. There is scant direct evidence of trees increasing pH. Montagnini (1995) reported several studies aimed at determining the impact of stands of several tropical and subtropical tree species on soil fertility and nutrient cycling on degraded ex-forest sites in Latin America. A few species increased soil pH (from ca. 4.8 to 5.2) whilst most increased the organic C% and cation concentration; all these effects should reduce the Al saturation of the exchange complex. In general, though, it is doubtful that tree litter can be a significant means of raising pH of naturally acid soils, since the amount of bases which could be available from litter decomposition would be relatively small compared with lime requirements. Sankaran et al. (1993) observed that soil pH within *A. auriculiformis* plantations was on average lower (ca. pH 4.7) than outside the plantation (ca. pH 5.0).

The likelihood of soils that support plantations becoming more acid will depend upon the rate of organic matter decomposition, patterns of base accumulation in aggrading biomass and N dynamics of the system. Before canopy closure, N and C dynamics in soils is probably the most active process affecting proton balance. After canopy closure, organic matter on the forest floor often continues to accumulate until the stand reaches maturity. During this phase, the system normally undergoes cycles of organic matter accumulation and decomposition associated with thinning operations. Accumulation of base cations in the vegetation and forest floor is the dominant factor causing a positive balance for protons in soils, although the net effects on soil acidity will depend upon factors like soil buffering range, rate of mineral weathering and the soil depth from which bases are taken up. Rhoades and

Binkley (1996) reported a decrease in soil pH in an Andosol (Hawaii) both under *Eucalyptus saligna* and *Albizia falcataria*. The soil under albizia had lower pH which was related to depletion of bases on the exchange complex. During the 8 yr of plantation growth albizia accumulated much larger quantities of bases in the aboveground biomass and forest floor than did the eucalypt. A significant amount of lost bases was compensated by weathering of minerals and by fertilizer additions.

Synthesis

Vast areas of both salt-affected and acid soils are presently either wasteland or underutilised. They can provide a suitable land base for tree-growing enterprises ranging from variably-sized plantations to farm forestry and agroforestry, subject to appropriate management of soil, nutrients and water, and correct choice of tree species and provenances. Plantations of fast-growing trees (e.g. *Eucalyptus grandis*, *Acacia mangium*) have already been established on acid soils in many tropical and subtropical regions of the world, but no extensive industrial plantations have so far been established on salt-affected land; rather farm forestry, agroforestry and community forestry are the main tree-growing systems on these sites. In Pakistan and India, *E. camaldulensis* and *A. nilotica* are favoured species for such systems.

The amounts of exchangeable and water-soluble Ca (+Mg) are important determinants of the impact of either Na (sodic) or Al (acidic) in these two types of soils. The Ca status of the soil is directly related to the vitality and growth of roots and thus to the uptake of water and nutrients by plants. Consequently, the frequency and intensity of water stress in plants growing on these degraded soils are major factors determining plant survival and growth rates. The two main issues that are common to tree-growing on these sites are: i) how to successfully establish trees and maintain acceptable growth rates; and ii) what type of impacts trees are expected to have on soil properties and soil water relations, and their implications for sustainable productivity.

Key elements to successful tree growing on salt-affected land are: i) maintenance of root-zone salinity at desired levels within the constraints of rainfall regimes and/or the quantity and quality of water available for irrigation; ii) use of appropriate planting methods (e.g. use of good quality seedlings, establishing mounds and application of gypsum and mulches); and iii) correct choice of species and provenances. As long as sufficient water is available for leaching, saline-sodic and sodic soils can be ameliorated by addition of gypsum, whereby Ca can replace Na from the soil exchange complex. Increasing the Ca supply in soils can also improve plant responses to salinity.

Strategically planted trees can lower elevated watertables beneath them and nearby on both dryland and irrigated land, but their impact is related to such issues as soil texture, depth to and salinity of the watertable and the density of tree planting. Long-term changes in root-zone salinity are less predictable, but either watertable fluctuations or leaching with rain or irrigation water will be necessary to maintain acceptably low levels. Evidence indicates that both salinity and sodicity can be reduced by tree growing and that choice of tree species can influence the degree of amelioration.

Future research efforts could best be directed to: i) selection of genotypes (and symbionts) for improved salt and waterlogging tolerance within key tree species and their incorporation into breeding programs; ii) determination of tree water use in response to increasing soil and water salinity; iii) development of options to manage salt within root-zones; and iv) linkages between landscape-scale models incorporating trees and farm management plans to optimise the placement of trees within catchments for improved water management.

The key elements of establishing fast-growing plantations on acid soils are the selection of suitable tree species and provenances, and management of soil P and Al by appropriate application of fertilizer, lime (and/or gypsum) and organic matter. Some attempts have been made to select tree species for acid soil conditions (e.g., screening of acacias) but additional research efforts are required for other plantation species, e.g. for eucalypts and indigenous species in the tropics. Management of N dynamics in soils in order to reduce leaching of N (as nitrate) is another issue which requires special research attention, especially in plantations of N-fixing trees, since leaching of base cations is linked with that of nitrates. Large areas of the humid tropics in high rainfall zones are now being planted with *A. mangium*. Additional work is also required on the nodulation characteristics of N-fixing trees under acid soils and opportunities for enhanced productivity through the use of acid tolerant symbionts.

There is very little evidence to suggest that tree-growing can reduce soil acidity. In fact, most evidence is to the contrary; this is related to losses of base cations during harvest, slash fires, erosion and site preparation. Excessive amounts of N (as nitrate) under N-fixing trees can also lead to N leaching together with losses of bases. Species variation in elemental composition of leaves may well influence opportunities for reduction in acidity, e.g. decomposition of leaves high in bases can reduce exchangeable Al in soils.

Acknowledgments

We wish to acknowledge John Simpson, Queensland Forest Research Institute (Gympie, Australia) for valuable comments on an earlier draft of the acidity section. We also thank ACIAR for providing financial support through their projects which provided valuable information used in this chapter. Sites depicted in Figures 14.1, 14.3 and 14.5 are managed by the Nuclear Institute for Agriculture and Biology Pakistan. Figure 14.4 shows data from a site managed by the Department of Land Development, Thailand.

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15

Towards Sustained Productivity of Tropical Plantations: Science and Practice

E.K.S. Nambiar
and A.G. Brown

Abstract

Even at current rates of per-capita wood consumption, there will be increasing shortfalls in wood supply, gross inequity in wood consumption between countries and continued threats to the environment by deforestation in coming decades. Plantation forests in the tropics will contribute more to world wood production as well as to mitigating land degradation. The increased production of wood can come from increasing both productivity per unit area and the land area under tree farms within a planned framework at a local and national level, and with environmental care.

There are diverse perceptions and expectations of sustainability. To progress, the elements of sustainable management should be integrated with practical goals of plantation forestry.

The wood yield of tropical plantations varies from about zero to very high levels. This significant variation is attributable to soil, environmental, physiological and especially managerial factors. A common cause of stress is poor management of soil and water, and nutrient deficiency. These factors can be manipulated to sustain or improve productivity. The volume of wood derived from a plantation is only an indication of its biological productivity; much of the primary biological production may be devoted to belowground tissues and processes. An understanding of carbon flow through the ecosystem and the factors which influence it is essential for good forest management and for ensuring long-term productivity. Management practices through which productivity may be influenced include the choice of site and species, methods of soil and stand management, the degree of vegetation control, protection from pests and diseases and choice of rotation length. The latter is particularly important, as harvesting and replanting operations, depending on the management, are both a hazard and an opportunity. Their frequency, has a large bearing on long-term productivity, especially in short-rotation forestry. There is no simple route to sustainable plantation forestry.

Plantation development should not take place in isolation but within a holistic framework for land use and ecosystem management. Proper integration of plantations with overall land use can assist multipurpose land use, whether plantations on their own serve more than one purpose or not.

In the last few decades, experience and research have provided a large body of knowledge of the biology and management of plantations in temperate environments. Many of the principles are relevant to plantations in the tropics. This knowledge however, must not be transferred uncritically but should be reviewed and validated in the context of the enormous biophysical variation and the management practices prevailing in subtropical and tropical environments. Much of the research methodology developed in temperate environments may be used in the tropics as a springboard for the research which management will require if the best results are to be obtained from the investment and opportunities which tropical plantations represent. The sound planning of that research including explicit attention to the factors that cause unsustainability will be critical for a desirable outcome.

The expanding extent and the potential of plantations to contribute to society is paradoxically exposing forestry and the associated industries to increasing scrutiny and controversy. Forest scientists have an unparalleled opportunity and obligation to provide balanced information and communicate it in the wider context of sustainability. Scientists must listen and stay in close touch with both community perceptions and economic realities.

THE PRECEDING chapters in this book have discussed in detail the biological and biophysical factors that determine productivity of forest plantations in the subtropics and tropics. This multidisciplinary approach by scientists in different fields has sought to ensure that the book as a whole is greater than the sum of the parts. The critical analyses in each chapter provide an understanding of the mechanisms and processes governing productivity, especially the interdependence of plantation productivity and soil, water and nutrient management. Although the chapters did not aim to provide prescriptions for management they have focussed on how the knowledge of ecosystem function has improved and can continue to improve management practices. They should assist researchers and managers to assess the prospects of plantation forestry in specific situations, to plan and conduct research, and to implement operations with the best available information.

In this chapter we draw together salient principles and relate them to the ideas, expectations and approach to sustainable forestry. We have elaborated on the need for plantation forestry in the tropics to be guided by clear and balanced goals which satisfy the economic, environmental and social aspirations of people in the context of overall use of the land in which the plantations are located. Critical analysis of barriers to successful management and of the aggregate value of the plantation are essential for achieving those goals. Plantation management should be supported by an evolving body of knowledge and effective means of applying research findings. For this we have pointed out the prospects of sharing information between temperate and tropical plantation forestry. The challenge ahead is not only to generate appropriate knowledge but to make that knowledge work for good management.

Sustainability in Context

Diverse perceptions

Ecologically sustainable development (ESD) is an idea that has caught peoples' imagination and raised expectations in many parts of the world. It is a logical and endearing idea placed high in national political agendas. Much of the debate about ESD has been and still is about forests, their ability to provide multiple benefits over the long term, their pivotal role in life-supporting processes and their value to the environment.

Debate on these topics is replete with concepts including 'ecological stability', 'ecosystem management', 'ecological management' and 'sustainable management' that are difficult to define and quantify. The conceptual problems of basing criteria of sustainability on constructs such as 'ecosystem health' and 'ecological integrity', and that such constructs do not reflect inherent properties of the ecosystem, have been discussed, for example by Lautenschlager (1995). Moir and Mowrer (1995) pointed out why sustainability is not an easy property to recognise or nurture. Ferguson (1996) suggested that 'Sustainable development (or sustainable forest management) might well be regarded as a mandala—a ritualistic symbol or icon of some desired but ill-defined future'. Ecologically sustainable forest management remains an elusive idea without clear definition or shared comprehension. Nevertheless the expectations for sustainable forestry and the political pressures on scientists, managers and policy makers to provide criteria and indicators for assessing sustainability are gaining momentum.

Plantation forests can be seen as a link in a continuum of forest estates (natural resources); the values of each link may be weighted on a scientific and rational basis to achieve a balance of environmental and production values (Nambiar 1996c; Chapter 1). Different forest estates in that continuum clearly have to be managed for specific needs. In the case of native forests there is an expectation that management should ensure multiple values (products)—economic, environmental, spiritual—in perpetuity without causing any changes in the structure and function of the forest ecosystem. Such objectives have led to social and political deadlocks.

There is however, greater clarity and consensus on the reasons for establishing and managing plantations, and their intended use. Plantations have been grown for a long time for a variety of purposes, and in a multitude of environments (Chapter 1). As their role has expanded they have acquired economic, social and cultural values, thus evoking diverse expectations in relation to sustainability (Nambiar 1996a, b). The expectations range from an insistence that plantations should mimic natural forests in structure and function and be managed to retain those attributes to more economically rational and pragmatic ones based on the view that plantations are a land-based business system which has to compete for capital with alternative investment opportunities. Several papers have recently discussed ecological, economic and cultural perspectives of these arguments, and confusion on the expected structure and features of plantations and their sustainability (e.g. Kanowski and Saville 1992; Rosoman 1994; O'Loughlin 1995; Sutton 1995; Nambiar 1996a; Nambiar 1996c).

Some countries have decided to use plantation forestry and wood-based industries as means to expand their economy and are vigorously pursuing domestic and international investments for that purpose. For example, 6% of GDP in New Zealand is obtained from plantation-based industry (O'Loughlin 1995). In Brazil, 4% of GDP is derived from forest industry which contributes a significant share of export income and creates four jobs per hectare of plantation (Ondro et al. 1995). In China, plantation forestry has become an important contributor to the economy of many regions. In India, which has stringent regulations on the area of land that can be owned by individuals or industry, the supply of wood for wood fibre-based industries is largely dependent on agreements between industries and farmers who own small parcels of land. Thus in many countries there are increasingly strong inter-relationships between plantation forestry, the economy, the environment and people's lives.

There has been large shift of the ownership of plantations from the traditional public service agencies to private sector businesses. In several developing countries plantations are largely privately owned. It is important to recognise this rapidly changing and dynamic nature of the ownership of plantations, and the economic motives and imperatives that drive plantation expansion worldwide: the basic reward is remuneration (monetary or material) from cultivating land, be the operators small farmers in India or Vietnam, or large industrial groups in Brazil or Indonesia. Investors in plantation forestry, small or large, consider plantation management principally as an exercise of property rights within a broader framework of environmental care and social responsibility.

Ideas on plantation management and the criteria for assessing its sustainability have roots in historical relationships. Firstly, because most native forests are managed by governments and plantations were historically promoted by governments as man-made forests, native forests and plantations were managed with a common set of values. Planted forests—mostly monocultures grown on short or medium rotations—are however very different in structure, function and purpose from native forests. Secondly, all but a few governments have abandoned their historical role of providing a 'sustained wood yield' and 'resource security' for the timber industry from a given geographic area. Sustained yield management for plantation-based industry has become a market-driven business option of individual enterprises.

'Codes of Forestry Practice', largely drawn up to manage native forest, have been applied to the growing of single species of trees on cleared forest land or ex-agricultural land on which agriculture may have failed. However, from a land management and silvicultural perspective, plantation forests are closer to farms than native forests, and wood harvests can be considered as another farm product. Large areas of eucalypt plantations being grown in China, managed on a 5–10 yr cropping cycle, are best described as tree farms aimed at providing one or more specific products. In Western Australia, many farmers have planted and are planting a small proportion of their land with trees with the objective of diversifying output and income, and in some cases for the associated benefit of salinity control (Shea 1993). Wood from these discrete tree farms is aggregated for industrial use. In some countries plantations have the potential to assist the sequestration of carbon and to partly off-set the rising CO_2 concentration in the atmosphere, for example, in New Zealand (Hollinger et al. 1993; O'Loughlin 1995). Land use decisions fostering plantations with multiple goals are bound to increase in several regions of the world, and strengthen the need for sound land management policies within an ecosystem context. However, plantation forests and tree farms are not wild forests in structure and function.

Interactive elements of sustainable land management

Plantations are managed with widely-varying intensity with the primary purpose of commercial wood production. However, there would be little future for them if management was driven by an extractive philosophy. Holistic, sustainable management of plantations should consider long-term biological productivity, and the environmental, social and economic factors linked with the business of forestry.

The impact of management on ecosystem sustainability can be viewed in several ways. In one model (Kaufmann and Linder 1996) ecological capability was taken as having restricted flexibility, and ecosystem sustainability was presented in relation to the degree of alignment between ecological capability and social and economic needs. That approach was modified (Nambiar 1996a, b) to examine the sustainability of plantation ecosystems (Fig. 15.1). Plantation sustainability is most likely if there is maximum alignment between key interdependent variables that include:

- ecological capability of the site
- intensity of management
- soil, water and other environmental values
- economic benefit and social goals.

There is no precise definition nor measure of ecological capability. In the context of this paper, this capability is bounded by the inherent soil and biophysical constraints, and the responsiveness of the soil to management inputs to increase productivity. It should take into account the genetic potential of the species and their interaction with the site environment. The relationship between management practices and their effect on production and environmental values is dynamic, and thus practices should be continuously reviewed in the light of new knowledge and opportunities for increasing production and profit. The intensity of management applied at a site should take into account the resistance, resilience and productive capacity of the soil as well as the impact of forestry on values of adjacent ecosystems. Larsen (1995) discussed some variables that should be considered in examining the ecological stability and sustainable silviculture.

Economic efficiency and profit is dependent on cost of production of wood, harvesting, transport and product development, and the market. A down-turn in the timber industry often leads to shortcuts in management, sometimes at a cost to sustainability. Profitability of industry and social justice may or may not always go hand-in-hand. However, economic viability and social goals are not separable.

Sustainable plantation management should strive to ensure maximum alignment of the variables indicated in Figure 15.1. For example, development of plantation forestry in relatively low-rainfall zones should not be at the expense of reduced water availability to other users. The alignments will never be perfect, because we are unlikely to have all the knowledge and management tools required to make decisions objectively. Nor is it likely that we will have a unified and universally agreed view of social and economic values—the measure of sustainability. Factors that continuously shape our views of sustainable management are many and changing, and we must be cognisant of the extraordinary range of biophysical and socioeconomic contexts of tropical plantation development.

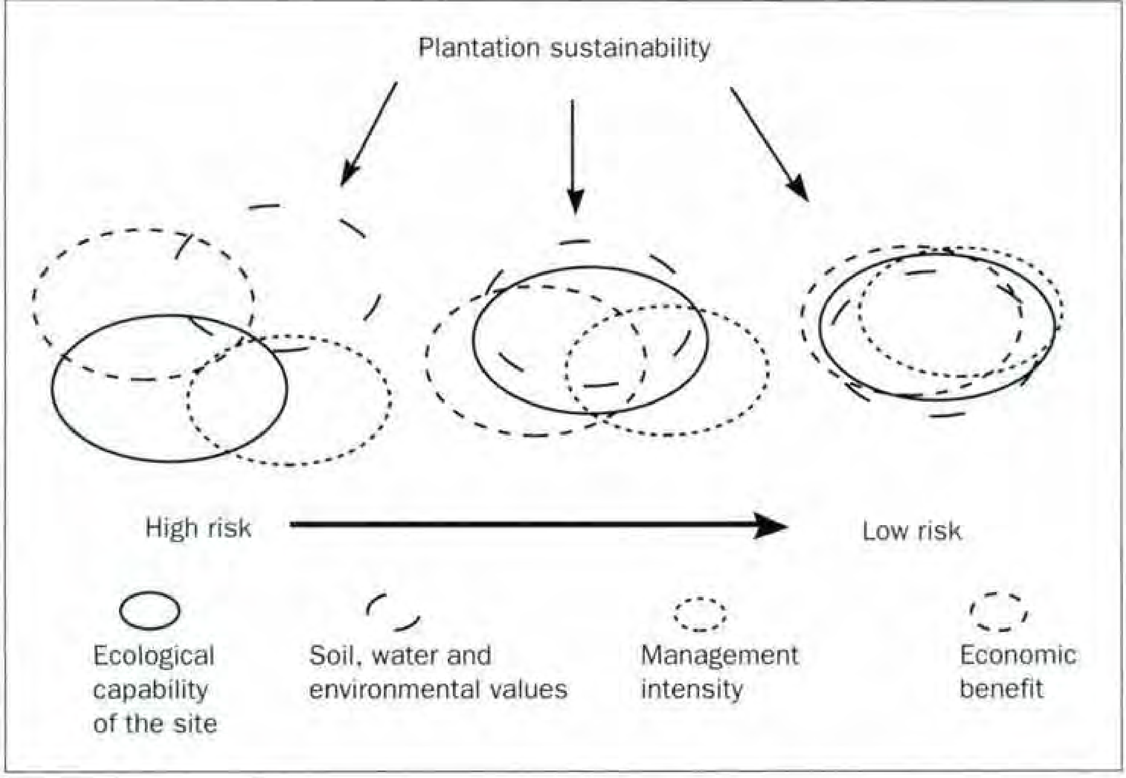


Figure 15.1 Interplay between ecological and management variables that govern the risk levels of sustainability of plantation forestry. (Adapted from Kaufmann and Linder 1996; Nambiar 1996a)

The Biological Basis of Productivity

Sustained yield

It is important to recognise the difference between sustained yield and sustained productivity of a plantation ecosystem. Sustained yield harvest (wood flow) is often compared to the accruing interest from an investment (asset). In plantation forestry, the asset is the total planted area of different age classes and the interest is the increment of merchantable stem wood. Stands of similar age on different sites may grow at different rates, depending on what is empirically described as site quality. The increment can be harvested sequentially by thinning and a final cut. Decisions on the diameter classes to be harvested and the age of the stand (rotation length) at which the final harvest is made depend largely on the products sought and commercial considerations. The frequency of harvesting and the nature of each harvest have dramatic impacts on the soil (see later and Chapters 5 and 10), on the biophysical environment at the site, and on growth (Chapters 3 and 6). Those impacts must be taken into account in developing management systems compatible with the long-term maintenance of productivity.

From a strictly commercial viewpoint, there is no immutable reason to increase or sustain wood yield of successive crops per se unless the ensuing product flow serves the economic goals of individual owners. However, sustained productivity of plantations and wise management of ecosystems are pillars of sustainable forestry and associated businesses. To develop sustainable management practices we need a basic understanding first of the processes that determine the biological productivity of plant communities in specific soil—environment niches, and second of the impacts of management practices on ecosystem processes and productivity.

Biological productivity

The potential maximum biological productivity of vegetation is determined by radiant energy. The extent to which this energy can be utilised depends on the genetic potential of the plants, soil productivity and climatic variables, especially rainfall and temperature. Potential productivity is always limited by stress (Chapters 3, 4 and 14) and thus management practices determine how and by how much stress is alleviated and genetic potential is realised. The extent to which a stand uses radiant energy for photosynthesis (growth) is directly related to canopy size and architecture. When stress factors (e.g. water shortage, insufficient nutrients, unfavourable temperatures, predation by other biota) do not limit growth, the relationship between light interception (through leaf area) and dry matter production is close. The full utilisation of a site's potential for biomass production occurs when and if the stand has attained and maintained the full leaf area which it can support (Chapters 6 and 7). The choice of the nature and intensity of management practices is thus an integral part of sustainable management.

One central issue we need to study for understanding and managing long-term productivity of plantation ecosystems is the pattern of carbon gain by the vegetation, the distribution of carbon in various components of the system, and the expenditure of carbon for maintaining life processes. This is important whether plantations are for industrial purposes or for the amelioration of land degradation. There is no single measure of productivity which is applicable for all purposes: gross primary productivity, net primary productivity or stem wood mass (or volume) increment are all attributes of productivity considered for various purposes (Chapters 7 and 12). Stem volume in itself is an incomplete measure of stem growth (carbon stored) for comparing species or effects of silviculture on stem growth because genotype, environment and silviculture influence wood density. The density of stem wood may vary more than two-fold between species (e.g. 400 kg m^{-3} for *Pinus radiata* compared to about 1000 kg m^{-3} for *Eucalyptus paniculata*).

The construction of a detailed carbon budget for an ecosystem is very difficult. Many of the required measurements (e.g. respiration by different tissues, translocation and turnover of carbon in roots) are difficult to perform, and scientists can so far only provide the best approximations using measurements and model simulations. The simulated storage and major flows of carbon in a *Pinus elliotti* plantation including understorey in a subtropical environment (Florida, USA) under normal rainfall conditions are shown in Figure 15.2. The important points are: (i) the amount of carbon stored in wood mass including branches is only a small portion of the total carbon storage in the ecosystem; (ii) processes in pine trees (the crop tree in this case), understorey and soil are interconnected through carbon flows, and (iii) a large proportion of the carbon is allocated to belowground processes.

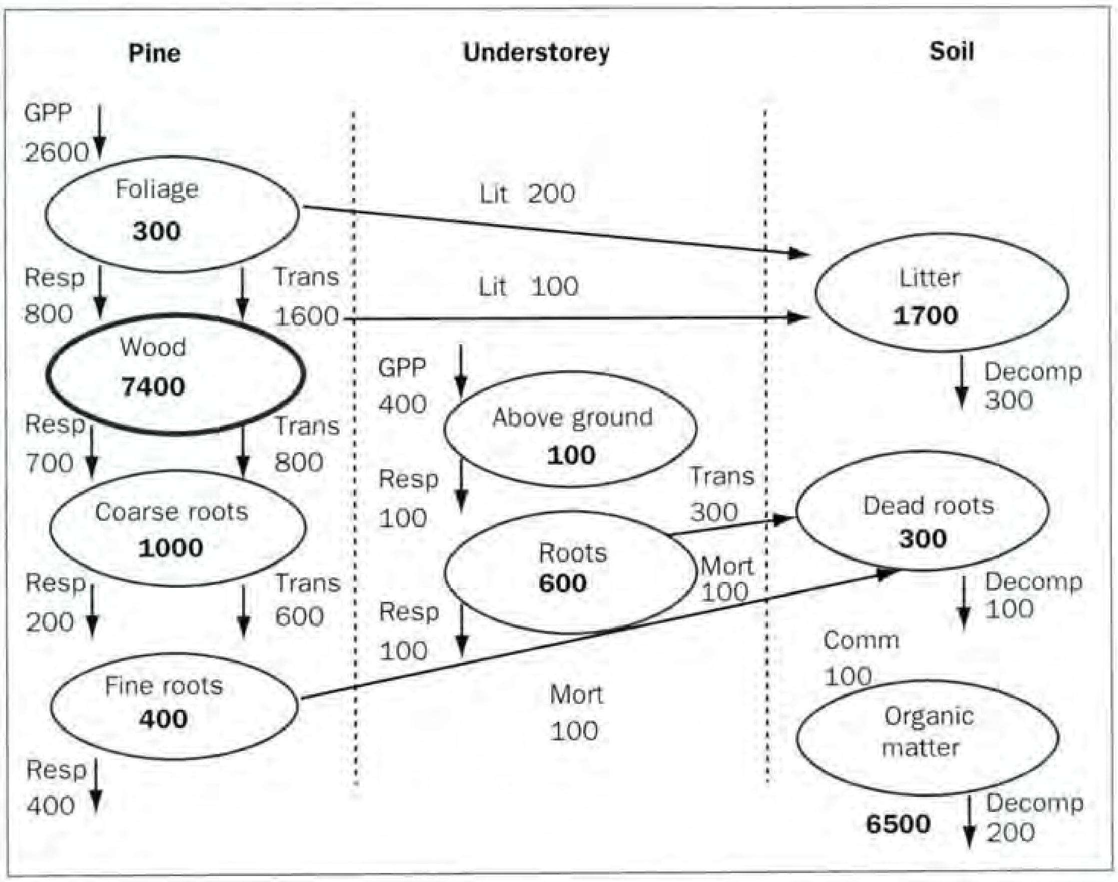


Figure 15.2 Storage (bold figures g cm^{-2}) and major flows (small sized figures g cm^{-2} yr^{-1}) of carbon in pine, understory and soil in a *Pinus elliottii* plantation in Florida, USA. Where: GPP = Gross Primary Productivity; Resp = Respiration; Trans = Translocation; Lit = Litterfall; Mort = Mortality; Comm = Communition; Decomp = Decomposition. (Adapted from Knight et al. 1994; Nambiar 1996a)

Ecosystem processes are driven by carbon flows in a dynamic sense. The storage, transfer and decomposition of organic matter are fundamentally linked with flows of essential minerals (Chapter 13). Soil organic matter is a major repository of nutrients (e.g. nitrogen); it has a profound influence on soil physical properties including structure and water-holding capacity, and it mediates critical biological processes. Also note that in this ecosystem (Fig. 15.2) a large proportion of the soil organic matter is derived from root turnover and that understorey roots contribute as much to soil organic matter as do tree roots. This is likely to be a common feature in other plantations (Chapters 8 and 13). The rates of litter and root production vary several-fold between species (Chapter 13), and this variation has a marked influence on the quantity and quality of soil organic matter. The age of the stand has a major influence on carbon flows, in ways specific to each species: net primary productivity rises rapidly up to a certain stand age then stabilises and eventually declines as the stand becomes old; the allocation of biomass to different components varies with age, as does the release of carbon through litter and mortality. Stand age influences stand structure (e.g. degree of canopy closure) and thus the dynamics of growth and mortality of other vegetation (Chapters 6, 12 and 13). It is clear that the economic yield represents only a part of the biological productivity of a plantation site. Processes that govern the flows of energy, carbon, water and minerals through the ecosystem are fundamentally coupled with the long-term biological productivity and hence sustainability.

The potentially high yield of fast-growing species in subtropical and tropical environments is commonly an important incentive for investment in plantations. However, yield expressed as mean annual stem volume increment (MAI) varies enormously (Chapter 1). For example, typical figures of MAI are 10–12 m^3 ha^{-1} yr^{-1} for *Terminalia ivorensis* in Nigeria, 15 m^3 ha^{-1} yr^{-1} for *Araucaria cunninghamii* in Australia, 15–20 m^3 ha^{-1} yr^{-1} for *Pinus caribea* var. *hondurensis* in Fiji and 40–60 m^3 ha^{-1} yr^{-1} for clones of *Eucalyptus grandis / urophylla* in Brazil. There are also many reports of very low yields from tropical plantations. For example, some commercial *Eucalyptus tereticornis* hybrid plantations in Karnataka, southern India, achieved growth rates from 0.2 to 7 m^3 ha^{-1} yr^{-1} at six yryr of age in regions which received rainfall ranging from 590 to 880 mm yr^{-1}, both the low yield in general and the variation between sites being attributed to soil water stress (Dury and Manjunath 1992). It is difficult to make useful comparisons of such yield data because management practices may have varied from extremely poor to reasonably sophisticated. They do show that the commonly-held association between 'fast-growing' plantations and the tropics is an over-simplification; trees can grow fast in the tropics only if soil and environmental conditions are conducive to rapid growth and the quality of management is high (Chapters 10, 11 and 13).

We have insufficient data to describe the relationship between yield and biological productivity and carbon turnover under the extremely varied conditions described in earlier chapters. Although long-term efforts devoted to understanding the cycling in temperate forests of carbon, water and nutrients have advanced our knowledge, many quantitative aspects of this subject remains uncertain (Kaufmann and Landsberg 1991). Uncertainties are greater in tropical plantations. This book has drawn attention to and illustrated the significance of assembling holistic information on carbon flow and organic matter distribution in tropical plantation forests.

The genetic base

The choice of species is a critical step in plantation establishment (Chapter 2). The choice has been strongly influenced by the suitability of the species for a particular end product (e.g. pulp), and the match between the environmental requirement of the species (often deduced from its native habitat and results in trials outside its natural range) and the environment of the plantation site (Booth 1996). There are several examples of the successful domestication of the exotic species in an environment substantially different from that of the native habitat. Large-scale development of *Pinus radiata* plantations in New Zealand, which has an environment very different from the Monterey Peninsula in California (the native habitat of *P. radiata*), is a striking example. When exotics are used the common assumption has been that with appropriate technology including selection, breeding and propagation the favoured species can be adapted to the sites of the intended plantation, and the supply of water and nutrients to the plantations can be improved by appropriate management. This assumption has worked in many cases, but an unsystematic approach has led to the failure of plantations in some instances. Because of the relative ease with which genetic gain can be captured via the choice of provenance and/or the use of seed orchards or cuttings, tree breeding has enjoyed significant success in application (Chapter 2). Some inter-specific hybrids (e.g. *E. grandis* × *E. urophylla*, *P. caribaea* × *P. elliottii*) have the desirable traits of coping with environmental stresses including drought, waterlogging and frost, and being resistant to pests and disease. Opportunities for genetic selection for planting in salt-affected soils appear high (Chapter 14).

While tree breeding and planting stock production can be expected to lead to continuous tree improvement, genetic gain can be fully realised only if there are matching improvements in site and stand management. Impediments to the capture of genetic gain cannot be ignored and therefore it is necessary to be conservative when predicting the benefit from tree improvement programs in the tropics (Haines 1995). Tree breeders need to address several questions to ensure long-term sustained productivity (Nambiar 1996a). For example, tree breeding is focussed on stem volume and form (economic yield) and as a consequence allocation of carbohydrate to the stem (i.e. towards a high harvest index). The critical issues of biological productivity, net primary production and the closely linked phenomena of carbon and mineral flow, fundamental to ecosystem function in the long term, and how the introduction of different species, provenances, families or clones at each crop cycle impact on these processes, are yet to be studied. Other issues to be addressed include the uncertain performance of genetically improved planting stock without intensive inputs to the site, the potential risks of narrowing the genetic base and the sweeping and poorly proven claims of dramatic increases in production via molecular biology. These latter claims ignore resource limitations, environmental risks and management constraints prevailing in the real world of tropical forestry (Nambiar 1996a).

Environmental effects and stand physiology

The tropical environment is a paradox: at one location it is conducive to rapid growth, elsewhere it is harsh and very stressful. A sound understanding of the interaction between environmental parameters and tree physiology, from the level of seedlings to stand, is essential for improving management (see Chapters 3, 6 and 7).

In many instances availability of water sets an absolute limit to growth at a site (Chapter 3). Even mild water deficits impede physiological processes and cause growth to slow, and under severe drought trees die. It is extremely important to assess the suitability of an area for plantation growth— the extent and probability of drought that may occur during the life cycle of crop trees is critical. Seasonal water deficit is common even in wet monsoonal climates. Methods for measuring and analysing soil water balance are well established (Chapter 5). Although the opportunity for managing water (because irrigated plantations are rare) is less than for managing nutrition, several soil water conservation measures and stand management practices can improve the availability of water to trees. What is urgently required is site-specific research to assess and measure how factors including soil profile features, soil and organic matter conservation, location of stands in the landscape, tree spacing, vegetation management, species and stand development influence the dynamics of water available to stands. Available water often has an over-riding effect on the nature of the response to changes in nutrition (Nambiar 1990/91).

Knowledge of physiological characteristics of genotypes which can make efficient use of seasonal water (when available) but also have drought tolerance can be valuable. In Chapter 6 it was suggested that such genotypes should be able to shed leaves when water stress increases above a threshold level but be able to quickly grow leaves and develop canopy when water is replenished, but we note that resource use efficiency is a complex concept to include in management (see later). A better understanding of the interaction between water, nutrition and plantation productivity is critical to good land management either from a production point of view (Nambiar et al. 1990), for salinity management (Chapter 14) or for managing the water resource in the forested land (Chapter 5).

There is little information about the dynamics of canopy development in tropical plantations, even of species which are being planted on a large scale (e.g. *Acacia mangium* in the humid tropics). Canopy development should be described in relation to leaf growth and longevity, shoot growth and geometrical display, and the dynamics of canopy maintenance through the rotation (Chapter 6). There is anecdotal evidence and field observations of sudden decline ('growth check') or loss of canopy at various stages of stand growth for which there are seldom valid explanations, although availability of water, nutrients or both is commonly implicated. Experience with temperate species shows that leaf area is a useful measure which integrates the effects of soil and environmental factors, especially water and nutrient availability, on stand growth. If the dynamics of leaf area are described quantitatively in relation to site resources, leaf area may be used to assess the condition of the stand and to make decisions on ameliorative measures (e.g. fertilizer application). Detailed knowledge about canopy development and the pattern of stand growth are also important in defining nutrient uptake and water use, and for developing appropriate silviculture for managing mixed species (Chapter 9), inter- and intra-specific competition and weed control, thinning and fertilizer application beyond the establishment phase, and for arriving at an optimum rotation length.

Root systems and below ground processes

In general, knowledge of root systems lags behind that of the structure, function and physiology of aboveground parts. This is simply because of the formidable difficulty of studying roots. Chapter 8 highlighted major deficiencies in our knowledge of belowground processes. Even after several elaborate and expensive studies in temperate forests designed to understand and quantify the nature of carbohydrate allocation to belowground parts, our knowledge remains restricted. There has been little systematic research on this topic in tropical plantations; although available data sets can provide some information they are inadequate for any detailed comparison and synthesis. There is very little information on the configuration, geometry and development of root systems in relation to site and stand growth, the basic prerequisite for interpreting nutrient and water uptake data and for refining management strategies (including competition control) for efficient use of site resources. Beneficial growth responses to selected isolates of mycorrhizae have been repeatedly reported in controlled experiments and in seedlings growing on P-deficient soils. However, reproducing such responses reliably under field conditions remains elusive. Innovative approaches to silviculture based on mixed species plantings may be possible in future, but progress towards such options will be faster if we can gain more knowledge about the way different species (including N-fixers) share site resources (Chapter 9). Nitrogen fixing plants may contribute N to an ecosystem, but build up of mineral N and leaching of N can lead to loss of cations.

Resource use efficiency

Some empirical studies suggest that some site and management practices (e.g. fertilizer application, spacing) improve water and nutrient use efficiencies (e.g. Eastham et al. 1990; Nambiar 1990/91). Resource use efficiency (RUE) is an idea often used without appropriate definition. Expectations for breeding for greater RUEs have been common and warrant some comments.

In breeding programs, the selection and testing of genotypes for economic traits are commonly carried out under conditions where the inherent constraints to growth at a site are minimised or removed by soil and stand management practices. Site preparation to increase water and nutrient availability, fertilizer application and weed control to minimise competition for site resources including light are common in progeny trials even if the intensity and quality of silviculture in the surrounding plantation are low. There are significant differences between species in the amount of nutrients produced per unit of biomass accumulated (Chapter 11). Large difference in conversion efficiency can be found between genotypes. Dalla-Tea and Jokela (1991) found a strong linear relationship (r^2 0.90–0.94) between the proportion of photosynthetically-active radiation intercepted by the crown and biomass production, but more interestingly, they found large differences in the conversion efficiency based on aboveground biomass increments between slash and loblolly pines: 0.47 and 0.81 g MJ^{-1} respectively. There are numerous reports of genetic variation in a range of morphological and physiological attributes and processes in trees. It is not surprising, in view of our knowledge of evolution and adaptation of plants, that researchers find interesting physiological differences between genotypes, and hold expectations for breeding varieties which are more efficient in using resources, in particular nutrients and water. Such expectations are often higher with tropical than temperate plantations because of the hope that such a genotype would reduce the need for high inputs (e.g. fertilizers) to increase productivity.

A critical analysis of the definitions, claims and simplistic notions of RUEs is warranted. Some key ecophysiological perspectives can be obtained from a recent review on RUEs (Sheriff et al. 1995):

- RUEs are simply ratios; they may be positively or negatively associated with productivity or have little relationship with it;

- Different RUEs may have opposing constraints, that is, a higher RUE for one resource may be linked to lower RUE for another;
- RUEs are mostly measured as instantaneous values at a simplified and small scale. The behaviour of a system at a large scale (stand level) and over a long term cannot be predicted by summing the outcome of one or two processes measured at a small scale. For example, photosynthesis measurements at a leaf level in seedlings may not be a useful predictor of genotypic behaviour at a stand level through time.

Productivity in the long term is influenced by many opposing and interacting process that regulate the carbon budget (Chapter 7) (Fig. 15.2). Productivity of most plantations areas is limited by more than one site resource (Chapters 4, 11 and 14). Furthermore, the genetic correlation between traits may be positive or negative, and from a practical point of view the addition of every new trait to breeding objectives adds complexity and cost to breeding programs and their application.

RUEs are measured and reported in so many ways that we have great difficulty in drawing together a cohesive picture from the data. In an earlier review (Nambiar 1984) it was concluded that nutritionists, physiologists and breeders alike are faced with the problem that we do not have a sound basis on which to accept or reject nutritional or physiological characteristics in breeding programs. That problem persists and we do not yet have a clear view of breeding for RUEs.

Managing Productivity

Ecosystem function and productivity are determined by a complex array of interactive processes related to soil, vegetation and environment, and several of those processes can be described quantitatively (Kimmins 1994; Landsberg and Gower 1997). Physical, chemical and biological processes in soils represent only a sub-set of those processes. However, they have overriding influences on water and nutrient availability for plantation growth and are fundamentally important to belowground processes including development and function of roots and symbiotic associations. There are no universally applicable conclusions about the impacts of site and stand management on soils and sustained productivity, nor should we expect any. Management practices impact in many ways that are site and situation specific (Chapters 4, 9 and 10).

Plantation management operations should ensure that the soil base is protected and that disruptions to ecological processes—carbon, nutrient and water cycles—are managed within known boundaries of resilience and amelioration of the particular ecosystem. In general, one can argue that risks to the soil resource base, to long-term productivity and to the environment can be expected to increase with increasing frequency and intensity of management interventions, and with higher production goals. The inherent productive capacity of soil determines the limits of its capacity to cope with depletion in soil fertility and other impacts of management (Chapters 4, 10 and 11). Similarly, as noted earlier, site water balance has an overriding influence on the growth responses achievable through manipulation of the soil nutrient supply.

The goal of commercial plantation forestry is not simply to maintain production at a level dictated by inherent constraints at a site, but to increase production. Productivity on many sites is below the potential and there are opportunities for increasing production, in some situations on a large scale, by appropriate soil and stand management practices (Dyck et al. 1994; Chapters 4 and 11). Sustaining production at a low level because of fear of the potential adverse impacts of technology will result in a lost opportunity to provide a solution to the world's growing demand for wood. It is not necessarily a sensible economic or environmental management strategy. The economic viability of forestry is dependent upon achieving growth rates appropriate to the species grown and the products required. It is unrealistic to expect that such a level of productivity will be maintained in perpetuity without adding nutrients to the site, either to correct inherent deficiencies in the soil or to compensate for depletion (Chapter 10, 11 and 13). The challenge then is to find a balance: strategies and methods designed to improve productivity in the long-term while minimising negative impacts on or off the site.

Productivity changes over successive rotations

When productivity of successive plantations at the same site is compared using stem volume as a measure of productivity, there is no consistent evidence of a 'second rotation decline' in temperate plantations (Morris and Miller 1994). South Australia's *Pinus radiata* plantations growing in podzolized sandy soils showed a decline in yield in the past, but the second- and third-rotation crops growing now are being managed at a significantly higher level of production than the corresponding first rotation. This has been possible through the adoption of improved silvicultural practices including organic matter retention, weed control, fertilizer application and genetically improved planting stock (Boardman 1988; Hopmans et al. 1993; Nambiar 1996c). Experience in Australia, New Zealand and South Africa shows the value of different management options for increasing and sustaining production in plantations. Furthermore transport of chemicals, pesticide or herbicide from plantations to waterways is rare in temperate forestry if management practices are carried out within prescribed guidelines (Neary and Hornbeck 1994). Such advances require a steady flow of scientific information, well-developed management skills and investment.

There are many questions about sustained productivity of plantations in the subtropics and tropics. The limited amount of published data do not point to yield decline (Herbert 1984; Evans et al. 1992) but it is probable that the cases of decline remain unpublished and the answer is unlikely to be a simple yes or no. Sound answers and solutions to problems will not come from *ad hoc* comparisons of stem yield from sites of successive rotations, as these seldom give insights into site productivity and factors that control it. Well designed, long-term productivity studies examining the effects of management on productivity and the processes governing it are needed in a wide range of plantation ecosystems (Powers 1990; Powers et al. 1990; Dyck et al. 1994). There are several sensible management options for increasing productivity if resources for investment are available, but we do not have clear answers to questions such as whether growth has been maintained or increased mainly through genetic improvement of planting stock, vegetation control or fertilizer use or; is long-term productivity perching, precariously, on a degrading soil base? Given the properties of tropical soils (Chapters 4, 5 and 11) and the impact of short-rotation forestry on soil nutrient reserves (Chapter 10) it would be a serious mistake to ignore the potential threat to sustained productivity of tropical plantations.

There is little information on the changes in net primary productivity (NPP) between successive crops at the same site in either temperate or tropical plantations. In order to understand the trend (changes) in the productive capacity of sites, we should measure NPP, or at least dry matter production of trees and other vegetation. One reason for this is the strong evidence that a large part of the production may be in belowground components (roots and associated symbionts) and the proportion of the production allocated belowground is greatly influenced by site factors (especially water and nutrient availability). Lack of information on biomass production and organic matter turnover between successive crops under a range of silvicultural regimes is a major limitation to our knowledge of sustained productivity. This is a priority area for research in order to develop long-term land management strategies.

All experimental approaches to test whether a particular plantation ecosystem is sustainable or not present inherent problems arising from the length of time and spatial variability encountered. Research of a complimentary nature, using process based experiments and models, can increase our knowledge and improve management options. For critical reviews of such approaches readers are referred to Kimmins (1994) and Landsberg and Gower (1997).

Management intensity, soil changes and productivity

In production forestry, there is no objective definition of management intensity or its scale. We can, however, describe one set of silvicultural practices as more or less intensive compared with another in terms of its expected impact on the soil and stand, in relative terms.

The most striking impact on soil and site environment, and hence on long-term productivity, can occur due to operations associated with harvesting, site preparation, planting and early silviculture. A single site preparation practice (e.g. heavy windrowing under wet soil conditions) can cause severe and lasting damage to the soil. An understanding of the resilience and properties of the soil is fundamental here. Of the many key properties and processes that are changed by forest operations, the most critical ones include the physical state of the soil, levels of organic matter, nutrients and nutrient dynamics, and competition for site resources between different components of the vegetation. However, the period of change between crop rotations also provides an opportunity for correcting past mistakes, to apply improved practices and to integrate planning and operations with due adherence to principles of ecosystem management.

The range and scale of intensity of various operations that can be applied during site preparation and establishment of the next crop is represented in general in Figure 15.3. A choice may be made from a variety of practices to suit a particular set of site factors and management objectives.

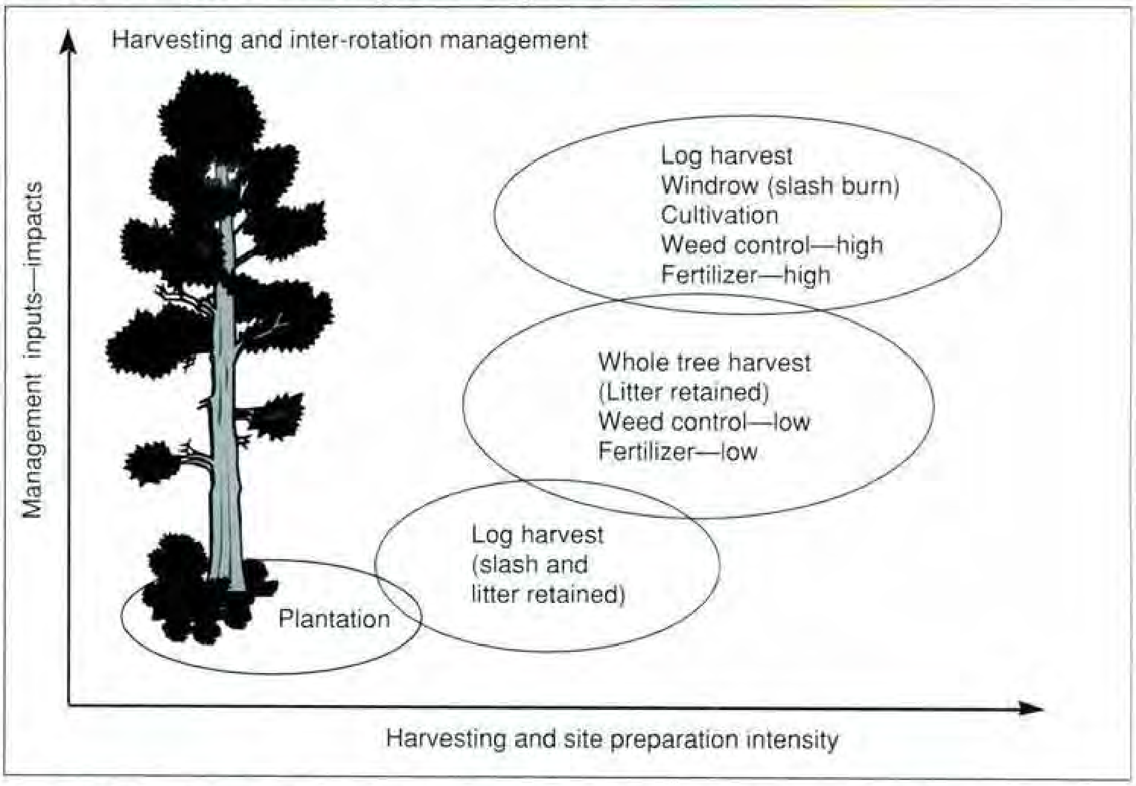


Figure 15.3 Intensity of site management during harvesting and the inter-rotation phase. (From Nambiar and Brown 1995; Nambiar 1996b)

In general, although site conditions and standards of management vary enormously, the scientific knowledge and field experience in warm temperate plantation forestry has allowed clear delineation of the worst and best practices, and methods for ongoing improvements in practices. Knowledge from research and experience with site-soil management practices has enabled development of practical methods for conserving site resources and improving availability of nutrients and water to match the uptake requirement of stands in temperate forestry (e.g. Nambiar et al. 1990; Dyck et al. 1994; Griffith 1994; Borschmann 1995). Now experimental studies focussing on impacts of management in a range of subtropical and tropical plantation sites, making the best use of the experience from warm temperate, fast-growing plantation systems, are urgently needed. Such studies should be designed with the dual goals of elucidating mechanisms and providing practical answers for management.

They should eventually provide data for constructing quantitative relationships between changes in soil properties and site productivity. Such relationships remain poorly established. For example, the dynamics of organic matter, including its rate of accretion and decomposition, long-term replenishment and transformation are recognised as fundamental factors for long-term soil productivity. However, direct evidence linking organic matter in soil and productivity is non-existent. There has been a growing emphasis on site management practices which favour maximum retention of organic matter (bark, slash and litter) during harvesting operations (Chapter 13), largely stimulated by the need to minimise nutrient depletion (e.g. Powers et al. 1990; Hopmans et al. 1993; Morris and Miller 1994; Smith et al. 1994). The treatment of slash and litter influences several factors including soil water availability and soil temperature, apart from the role of slash and litter itself as a nutrient store (Smethurst and Nambiar 1990a, b). In some instances slash retention inhibits weed growth. The nature of these interactions varies with the environment. However, the questions remains: does organic matter conservation and minimum cultivation replenish soil organic matter and increase site productivity? The long-term trend in the quantity and quality of organic matter under plantations of the type now grown in the subtropics and tropics needs to be studied and quantified (Chapters 9 and 13).

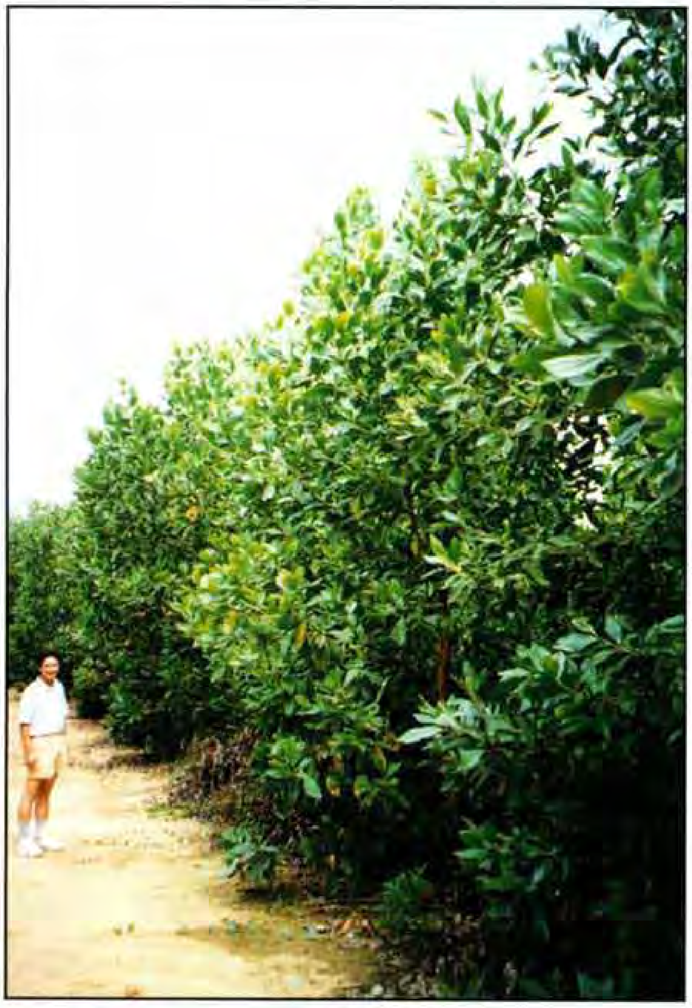
Johnson (1992) reviewed the literature, largely based on temperate forests, and concluded that there is no general trend toward lower soil carbon with forest harvesting, unless harvesting is followed by intense burning or cultivation. The potential loss of carbon from soil as a consequence of site management may, however, be very critical in short-rotation plantations on tropical soils. Will the carbon levels in soils be replenished during the rotation period? An insight into the fate of soil carbon in relation to land use in the tropics is provided by Tiessen et al. (1994). These authors compared the changes in topsoil carbon in a chernozem prairie soil in Canada and ferralsols converted from native tropical forests to agriculture. Results showed that clearing the native ecosystems for agriculture and accompanying land management practices led to large reductions in soil carbon, and pointed out that 'at the Brazilian and Venezuelan sites' agriculture rapidly became non-viable without fertilizers due to loss in soil fertility. The mean residence time (MRT—the inverse of the decomposition constant) for the turnover of carbon for the Canadian, Brazilian and Venezuelan sites was 98, 11 and 2 yr respectively. In the ferralsols a significant proportion of organic matter and associated nutrients are sequestered in lateritic nodules and do not contribute to nutrient cycling.

Thus the relationships between primary productivity and organic matter addition, and processes determining organic matter depletion and replenishment as affected by silviculture, are important issues for further research.

Another problem in improving management decisions is our lack of capacity to reliably predict the response of an individual stand to silvicultural input, unless the stand exhibits obvious nutrient deficiency. Systematic research on soils can, in some cases, provide broad guidelines on the levels of 'nutrient availability' required to correct nutrient deficiencies (Chapter 11). Lack of reliable quantitative relationships between any arbitrary measure of 'available nutrients' and growth does diminish the value of soil-based parameters as a predictor (Chapter 11). While mechanistic models to predict growth may provide a practical management tool in the long-term, no such tools exist currently. Simple and reliable predictive models that encapsulate present knowledge of soil and stand factors which determine productivity are needed (Chapters 3 and 11).

Because there are several conceptual and experimental constraints to direct measurement of long-term productivity and in interpreting those measurements, it has been argued that ecosystem stability should be monitored by alternative means using indicators. However, any such indicators that we may discover, if they are to be useful and reliable, should represent soil processes that are quantitatively related to site productivity. Given the complex interactions involving soil, the biophysical environment and species that determine productivity, simplistic notions of indicators should be treated with caution (Nambiar 1996c).

Plantations of species such as *Acacia mangium* or *Gmelina arborea* can grow rapidly, as is illustrated on these sites formerly occupied by secondary rainforest. Weed control by one or two herbicide applications was important. The challenge for research and management will be to maintain productivity of such sites in the long term. The photographs below show that plantations of *A. mangium* planted without cultivation established quickly. (Photos: E.K.S. Nambiar).



Fifteen months later, the canopy was closed, and a significant litter layer was developing.
(Photo: E.K.S. Nambiar)

The ability of *Gmelina arborea* to grow rapidly is illustrated by this 5-month-old stand.
(Photo: E.K.S. Nambiar)

Plantations, Water and Land Use

Sustainable use of cultivated land (including tree farms) can be advanced not by the isolated success of individual enterprises in a plantation area but by the performance of all enterprises—small and big—and the effect of their collective interaction with the local or regional environment. Proper integration of plantations within overall land use can promote multipurpose land use, whether plantations on their own serve more than one purpose or not.

As plantation forestry expands we should expect new questions and uncertainties to arise from the conflicting societal needs. Concern about the potential impact of plantations of exotic species on catchment and regional water balances is a well-known example (Chapters 5 and 7). This concern has become a constraint on access to land for plantations in some regions, for example in South Africa which has been successful in developing plantations of exotic pines, eucalypts and acacia. That country now faces a dilemma in land use decisions: the predicted demand for water will increase by 44% and that for wood by 16 M m^3 in another 10–20 yr (Dye 1996). Dye has offered a number of solutions, and options for the balanced development of plantations based on detailed research on tree water use and hydrology in a number of ecosystems in South Africa.

Concern about the impact of plantations on water use at a catchment or regional scale has stimulated important research (e.g. Calder et al. 1992; Calder 1996; Lima et al. 1996 and in press; Teskey and Sheriff 1996) (see also Chapter 5). Results from these investigations can improve the basis for making land use decisions. For example, long-term hydrological research in Karnataka (southern India) and elsewhere shows that transpiration rates of *Eucalyptus* spp. are likely to be similar to those of other species except in situations where species of *Eucalyptus*, which do not link stomatal regulation to atmospheric humidity deficit, are growing in areas where atmospheric demand is high and there is plenty of water in the soil (Calder et al. 1992). Furthermore, interception losses by eucalypts are likely to be less than those by other tree species of similar size and stocking in the stand. It is also clear that bigger trees transpire more water than smaller trees whether they be *Pinus radiata* growing in South Australia (Teskey and Sheriff 1996) or *Eucalyptus tereticornis* growing in southern India (Calder 1996), illustrating the relationship between growth and transpiration. Based on long-term studies of a fast-growing *Eucalyptus grandis* plantation in Sao Paulo in Brazil, Lima et al. (in press) concluded that long-term management of plantations is possible without adverse impact on catchment water yield and quality. The long-term research project 'Fast-growing trees in Karnataka' helped to allay the specific fear that eucalypts draw directly from ground water (ODA Annual Report 1994). Kallarackal and Somen (1992) carried out a comparative study of the water use characteristics of three tree species in Kerala, southern India. They compared a fruit tree species, cashew (*Anacardium occidentale*) naturalised in Kerala since 16th century with timber species acacia (*Acacia auriculiformis*) and teak (*Tectonia grandis*). They found that plantings of acacia in sites previously occupied by teak would increase annual evapotranspiration (teak drops leaves and reduces water use during periods of drought), and cashew consumed substantially more water than acacia and could have been extracting water from the phreatic aquifer in summer months.

There is need to study further the physiological mechanism including rooting patterns of key plantation species under different environmental and site conditions of water availability. Sweeping conclusions about the adverse impacts of plantations on water, often echoed in the popular press, are seldom substantiated by evidence (Kallarackal and Somen 1992; Calder 1996; Lima et al. 1996), and claims of 'water-mining' by exotics need to be tempered with site and species-specific data. The establishment of tree farms and their management strategies (e.g. proportion of land planted with trees, choice of species, rotation length, thinning regime) should be carefully considered in relation to overall land use and associated vegetation.

Plantations may help to restore the productivity and biodiversity of degraded forest land in tropical regions (Parotta 1992; Fimbel and Fimbel 1996; Lugo 1996 and in press). The role of trees in changing the properties of soil in the long-term is a topic of much importance, yet poorly studied in any systematic manner.

The Way Forward

Setting goals

One practical way of advancing forestry is to integrate the elements of sustainability with the goals of plantation management. The primary intended use of most plantations is wood production, just as the primary purpose of agriculture is food production; both forms of land use must be on a sustainable basis. Sustainable agriculture was defined by the Australian Standing Committee on Agriculture (Hamblin 1992) as the use of farming practices and systems which maintain or enhance the economic viability of agricultural production, the natural resource base, and other ecosystems which are influenced by agricultural activities. A parallel definition of sustainable plantation forestry would be (Nambiar 1996b) as a land use practice and a tree farming system which maintains or enhances the economic viability of wood production for a variety of end products, the natural resource base especially soil and water, and other production systems (e.g. including crops and animals) that may be integrated with tree farming.

Nambiar (1996c) proposed that the goals of plantation management should be to ensure that:

- the trend in plantation productivity is non-declining or positive over successive harvests while maintaining and enhancing the quality of the soil resource base;
- plantation management practices per se do not adversely affect the environment; and
- plantation forestry is economically viable and contributes to prosperity of local people.

Progress towards these goals can, in principle, be monitored. To achieve these goals all practitioners of plantation forestry should be accountable through values shared with the community, necessary regulation including self-regulation where appropriate, and the implementation of outcome-oriented codes of plantation practice. In the context of these goals, the objectives of sustained yield (wood production) and sound ecosystem management go together. The significant areas of plantations established for soil conservation (e.g. casuarina planting in China) and for other land reclamation purposes (Chapter 14) have the same biophysical attributes as wood production plantations, and in most instances they are periodically harvested and replanted

The route to sustainable plantation management is neither easy nor rapid. It can only be gradual and stepwise through concerted action by a coalition of all parties: people, industry and Government. Ferguson (1996) pointed out some of the critical needs for achieving sustainable forest management: They include: effective institutions—legal, institutional or market based; rational allocation of the land base; holistic land-use planning and careful analysis of conflicting needs; a hierarchy of operational planning from the level of sites to regions; effective codes of practice which explicitly lay down standards of environmental care and responsibility for compliance; recognition of property rights and public participation.

Recognising unsustainability

Sources of risks

One important step towards achieving the goals is to clearly recognise and contain the sources of risks. We should ask the questions what would make plantations unsustainable and how would these factors impinge upon management decisions at various levels: for example from a management unit (small scale) to a regional scale. Decisions and prescriptions that promote maximum conservation of organic matter and nutrients at a site after harvest would apply at a management unit level; issues related to the extent of planting in a region and its impact on overall land use (e.g. protecting and sharing of water resources) can be addressed only at a regional scale, and matters concerning the economics of forestry and social justice are often addressed at a national level.

What would make plantation forestry unsustainable? The answers to the question include:

- Loss of soil quality: initiation or acceleration of soil degradation processes which decrease productivity and increase costs of amelioration.
- Adverse environmental impacts: off-site negative impacts including any affecting the quantity and quality of water in the ecosystem.
- A weak or inappropriate genetic base: genotypes that are inbred or unadapted to changing soil properties.
- Threats from pests and diseases: an issue needing continuous monitoring and integrated management plans.
- Poor management: in our view, the single most common reason for failure and which may outweigh the lack of scientific knowledge per se as a threat in some regions.
- Poor economic performance: when investment in plantations does not provide an attractive return, 'extractive' and unsustainable practices tend to be rationalised for short-term relief or gain.
- Lack of social justice and sharing of prosperity: this is not unique to plantation forestry, but needs sensitive action because industrial forestry affects land, water and employment of rural poor and can be seen as a threat to land-based subsistence.

The introduction of plant genetic resources to new environments (like human immigration) has been an integral part of our civilisation. It has been dynamic and continuous, creating new opportunities and revealing new horizons as well as problems. Eucalypts, which are largely indigenous to Australia, have been tried in more than 110 countries, with notable success in some. There is clearly no universal conclusion about the merits and demerits of eucalypts or any other species. The debates about 'exotic' trees have often lost sight of this. Nor should the introduction of exotic species be pursued while neglecting indigenous flora and its potential for use in plantations. Similarly, while we should not place undivided faith in monoculture, we must ask where is the substantiated evidence of their doom? Informed discussion of these and other questions is essential in both formulating appropriate land-use policies and in planning relevant supporting research and development activity. The scientific uncertainties about ecosystem processes, the dynamics of social and political ideas, and the conflicting history of native forest management often colour debate on plantation forestry. It is not uncommon to find that accounts of perceived and real negative impacts of plantation forestry are widely disseminated, while achievements are ignored.

Research and the application of research findings

Structural (institutional) barriers

The extraordinary diversity in the physical and biological characteristics of plantations in the subtropics and tropics has been a recurring theme in this book. Great variation can also be found in the quality of management in the field. These variations, compounded by social and economic factors, can provide formidable barriers to sustainable operations. The identification of the most important research themes among competing and pressing problems, and the successful application of the results of research in practice, are no small challenge; examples of the difficulty are described by Ng (1996).

Advances in forest management have been characterised by slow but steady incremental progress over a long time, not through dramatic breakthroughs in science or quantum leaps in application. Reliable answers to key research questions on even short-rotation crops of trees require research which takes a decade or more. Sustained productivity of plantation forests in the tropics must be underpinned by sustained research efforts. In a general sense, these efforts are unfortunately very inadequate in some countries, and at best marginal elsewhere (Nambiar and Brown 1995).

The generic problems we have observed in a number of countries include:

- Lack of cohesive strategic plans linking problems in the field, the input of managers and research project selection.
- Mismatch of resources and priorities (e.g. the establishment of an elaborate molecular technology laboratory without the underpinning of a breeding plan; poor information on soils of the plantation estate).
- Lack of a conceptual and institutional framework for fostering a multidisciplinary approach, even when skills in more than one discipline are available.
- Alienation between researchers and managers despite the evident importance of doing practical, problem-solving research. Some tropical countries rely greatly on international assistance for their research, but even when such support is provided the lack of a cohesive plan among relevant agencies, national and international, and the absence of a shared vision and priorities are all too common.
- An acute shortage of resources, infrastructure and trained staff for research.
- Poor reward and working conditions for researchers.

Methodology advantage

Do we need new methodologies to study the productivity of tropical plantations? Several chapters in this book argue that the methods (in terms of equipment, experimental approaches, measurements and models) for acquiring process-based information in the tropical environment on several key issues are available and are transportable.

Furthermore, although the tropical native forests cover an extraordinary diversity of plant species with distinct ecophysiological behaviour and complex community-level interactions, a substantial proportion of the present and planned plantation forestry is based on a few genera and modest number of species. This concentration can considerably assist the focussing of strategic research on a few species and the gathering of data comparable across sites. Generic knowledge gained from these species can be built up to explore the behaviour of additional species as required.

Data on readily accessible parameters (e.g. basic climatic data, sequentially measured biomass data, relatively simple information on available water etc.) can be obtained from studies which may have been designed to improve local management prescriptions. Such information may be used with the aid of models to obtain greater insights into ecosystem function.

Chapters in this book also show that where information specific to a particular tropical ecosystem is lacking, experience and knowledge of temperate plantation forestry and especially lessons learned from warm temperate and Mediterranean regions can be profitably used, along with some basic knowledge of soils, environment and species behaviour in a specific tropical region, to develop interim strategies (best, first approximations) aimed at sustained productivity. However, that information should not be copied and followed uncritically.

Conclusion

Preparation of prioritised lists of research problems without the interactive involvement of managers is a recipe for failure in the application of results in the future. Furthermore there is an extreme range in the state of development of plantation forestry among tropical countries; from embryonic development in reforestation to specialised, vertically integrated, international-scale forestry and forest product industries. Throughout this book authors have reported what their analyses have identified as key research issues for the future. In a number of instances, using available information, they have proposed principles that should guide improved management and assist development of new management options. The sorting of the research issues into a cogent, prioritised and globally valid set is a daunting task. An important reason for this is the immense diversity in the subtropical and tropical environment and the variation in scope, scale and purpose of tree plantations. These considerations undoubtedly call for site and situation-specific research. For example, as much of the demand for fuelwood in the tropics is in seasonally-dry or arid environments where industrial plantations or associated industry are few or in their infancy, the provision of fuelwood and industrial wood generally has somewhat different problems and research needs.

The success of a few genera in plantations has led to their use in many situations beyond their natural range. As the tropical tree flora becomes better known, the potential of additional species and genera to be grown in plantations will be recognised, and the choice available to forest managers and landowners will correspondingly increase. It is inevitable, however, that many plantations will still consist of exotic species because of the varied adaptability of species for such use. There is thus no advantage in concentrating research on indigenous species in the expectation that they will somehow be 'better' than exotics.

Plantation forestry in the tropics is already significant, and expanding rapidly. Extensive areas have been harvested and re-established once or twice. Decisions needed in managing these stands today will not await the arrival of precise knowledge tomorrow. Mistakes, if made at the time of establishment of a plantation, are not easily rectified. Forest development policy needs to be based on sustainable production principles. This situation must be grasped by scientists. Should we take the most cautious view until we are satisfied about the answers to many questions about sustainable management of plantations, or should we try to influence the course of events by offering pragmatic advice? Will an over-cautious approach (based on the view that little is known) advance science or practice? There are overwhelming reasons for a closer partnership between scientists, managers, land owners and the wood-based industry in many tropical countries.

Acknowledgement

The contents of this chapter are partly based on papers presented to meetings including: Nambiar and Brown 1995, Nambiar 1996a, Nambiar 1996b and Nambiar 1996c. It has also drawn on the contents of chapters in this book, discussion with many colleagues and our personal experience in subtropical and tropical plantation forestry and associated institutions.

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