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Selection for Water-use Efficiency in Grain Legumes

Report of a workshop held at ICRISAT Centre, Andhra Pradesh, India, 5–7 May 1993

Editors: G.C. Wright and R.C. Nageswara Rao

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Preface

ACIAR supported a major research and development project on groundnut improvement in Indonesia over six years from 1985 to 1991. This project developed technology to improve management of the crop and identified a range of constraints worthy of further investigation. Outcomes are summarised in ACIAR Proceedings No. 40, 'Peanut improvement: a case study in Indonesia'. Drought, bacterial wilt and peanut stripe virus were among the constraints identified, and ACIAR has supported further work on these problems.

Drought and plant water-use efficiency (WUE) are important in determining crop yields, particularly in rainfed environments. ACIAR Project No. 9216, on WUE of food legumes, aims to develop methods for using carbon isotope discrimination (Δ) to measure WUE and facilitate identification and promotion of drought-tolerant lines of groundnut, soybean, cowpea, navybean and chickpea in India and Australia.

As well as the development of WUE technology and the promotion of food legumes, the project also provides experience in the management and execution of a complex, multi-locational study over some seven sites in India. It was decided to hold a workshop at project initiation to discuss and refine a common methodology to be used by all cooperators across all sites, in order to promote common understanding and to ensure data collected were compatible for later, common analysis.

The workshop was successful, with many differences in opinion and understanding being resolved, and a common experimental methodology being agreed upon, **before the experimental work had started.** It has ensured that everyone involved has had a chance to contribute to agreed methodology, and that data collected from all sites will be compatible and amenable to combined analysis. It is hoped that this excellent start will be reflected in enhanced project outputs, and that the workshop may serve as a model for the initiation of other complex, multi-location studies involving many sites and cooperators.

The smooth execution of the workshop was due to excellent support and facilitation by ICRISAT, ICAR, QDPI and ACIAR, for which all participants are grateful.

Colin Piggin
Research Program Coordinator
Crop Sciences
ACIAR

Address of Welcome

ON behalf of ICRISAT's management I welcome you to this workshop which has the important task of laying the foundations for a collaborative research project on water-use efficiency (WUE) in groundnut. This project will involve scientists from ICAR, ACIAR and ICRISAT, and I am sure that you will all do your best to ensure that it becomes a model for this type of collaborative work.

Much of the world's groundnut production is from the semi-arid tropics (SAT) and it is not surprising that drought should figure as one of the most important production constraints of this largely rainfed crop.

In the international workshop on groundnuts held here in Patancheru in 1991 we discussed production problems with scientists from many parts of the world. That workshop recommended that research on drought should receive high priority and that research on WUE should be initiated.

In 1992 we prepared a medium-term plan for ICRISAT's research for the period 1994–1998. This involved in-depth consideration of many research themes on all of our crops, taking into consideration all available information and seeking the opinions of our partners in the national research systems (NARS). Themes were prioritised on the basis of efficiency (net benefit/cost), equity (poverty and gender), internationality and sustainability. On this basis, research on drought in groundnuts to be conducted at ICRISAT Centre, in West Africa, and in Southern Africa ranked 19th in the consolidated list of all ICRISAT's research themes.

The project on WUE in groundnut that we will be discussing here should provide a unique opportunity for interdisciplinary and inter-institutional research on perhaps the most difficult problem faced by farmers of rainfed groundnuts. The approach, which is based on selection of groundnut genotypes for specific traits that relate to WUE and hence drought tolerance, should provide breeders with a valuable tool to select and propagate varieties of groundnut with improved resistance to drought.

I understand that research will be conducted at six centres in India and I am aware that Dr M.S. Basu from ICAR and Dr R.C. Nageswara Rao from ICRISAT have done a great deal of work to ensure that scientists at the cooperating stations will have the equipment and facilities needed to play their parts in the project. The present workshop is also part of this preparatory exercise providing an opportunity for you to become acquainted with the technology involved, share your knowledge on drought research, and develop a consolidated work plan to be followed by researchers across the various locations.

I again would like to welcome visitors to ICRISAT and hope that you have a productive and pleasant time during the workshop.

D. McDonald
Director
Legumes Program
ICRISAT
Andhra Pradesh
India

Cooperation between ICRISAT and ACIAR

My ICRISAT colleagues and I welcome all of you to this workshop on water-use efficiency (WUE).

It is highly appropriate that we meet to discuss this topic, particularly methodologies for selection of grain legume genotypes with high water use efficiency. Dr McDonald has already indicated that the theme of drought is very important for ICRISAT in terms of both current and future emphasis. Of the 92 research themes that we have identified as our core research portfolio for the coming five to six years, eight concern drought-related problems. Three of those themes relate to legumes, three to cereals, and two to both cereals and legumes.

A brief outline of each of the eight themes will give you a feeling for the importance ICRISAT places on drought-related problems.

1. *Drought affecting chickpea.* This theme ranked no. 3 on the list of 92 priority themes. The research will be focused primarily on work here at ICRISAT Centre.
2. *Drought in groundnut.* This was ranked no. 19 and will involve research here at ICRISAT Centre in collaboration with ICAR institutions, at the ICRISAT Sahelian Centre (ISC) in Niger, and at the Southern African Program in Malawi.
3. *Water deficit.* This priority theme, ranked no. 29, is a component of the Resource Management Program, and will be based primarily here at ICRISAT Centre.
4. *Water deficits in sorghum, pearl millet and groundnut.* Also a theme in the Resource Management Program, this work will be focused in Africa at the ISC and in ICRISAT's sorghum improvement program in Nigeria. It ranked 37th of the 92 priority themes.
5. *Pigeonpea.* Ranked no. 47, this work will be conducted at ICRISAT Centre and in our Eastern African Program out of Nairobi.
6. *Pearl millet.* This sixth theme on drought, ranked no. 59, is in the cereals program. Work will be carried out at four locations: ICRISAT Centre; ISC, Niamey, Niger; the Eastern African Program, Nairobi; and the Southern African Program, Malawi.
7. *Sorghum, pearl millet and finger millet.* This work on drought-related problems, ranked no. 63, is another component in the Resource Management Program. It would be focussed in southern Africa.
8. *Sorghum.* The eighth theme on drought is sorghum, which will be in the Cereals Program and focused at four locations: ICRISAT Centre; the West African Sorghum Program; the Eastern African Program; and the Southern African Program.

So it can be seen that drought is very much a multi-location theme. I think these drought themes will give you a good idea of the priority that we have accorded to this particular constraint. It is especially pleasing to me to be associated with this meeting focused primarily on groundnut because it is building on some research that, in an earlier incarnation, I was indirectly associated with, when I was involved with ACIAR in Australia prior to rejoining ICRISAT about 20 months ago.

I recall the then Director of ACIAR, Dr Jim McWilliam, thought that the work that was being conducted on carbon isotope discrimination at the Australian

National University (ANU) by a bright young scientist by the name of Dr Graham Farquhar was worthy of support. Dr McWilliam felt that if the carbon isotope discrimination technique could be shown to be well correlated with crop WUE, it could provide plant breeders with an easily measured parameter for utilisation in crop improvement programs aimed at enhancing genotype performance under drought. I would like to acknowledge the role that Dr Jim McWilliam, in particular, played in lending some strategic resource support and encouragement to Dr Farquhar who I think was instrumental in bringing forward the idea of using this carbon discrimination technique to the point which it has reached today.

This case represents, I think, a good example of the approach of organisations such as ACIAR in identifying what we might term 'blue sky' research. At the time ACIAR decided to support the research at the ANU, it was not clear whether the technique was fully proven and if it could be usefully applied. I feel that all research organisations, including ICRISAT, need to have an element of 'speculative' support for this type of research within the framework of a broad set of priorities that has been established. I am especially pleased as Director General of ICRISAT to see us building on the early support that ACIAR provided through the work of people like Graham Farquhar and now others in the Queensland Department of Primary Industries (QDPI). I am delighted that we are pursuing how we might generate spillover effects which were originally envisaged when the support was provided to Graham Farquhar and his colleagues.

ICRISAT has a number of linkages with ACIAR. We have collaborated on germplasm collection, particularly in 'para sorghums' which were a valuable addition to the germplasm bank from Australia. I believe that they had traits related to insect pest resistance. We had linkages in the international groundnut drought nursery trials in Indonesia through ACIAR. We had considerable collaboration with ACIAR in the area of viral diseases of groundnut, and acknowledge the collaboration between QDPI and ICRISAT which was effected by the late Mr Keith Middleton.

The devolution of CGIAR responsibilities to ACIAR has significantly arisen because of a very favourable parliamentary review that ACIAR recently received after 10 years of operation. I have not seen a report by a parliamentary review which was as favourable as that one delivered on ACIAR. I think this speaks very highly of the Centre. The fact that it is also responsible for multilateral aid in the area of agricultural research allows a new window of opportunity to us in the international centres to develop with them, what we might term 'consortia', involving trilateral linkages and partnerships whereby the complementarity between the bilateral program and the multilateral linkages that ICRISAT offers can be developed and pursued. I hope that we can consider the particular project on water-use efficiency in groundnut as a pioneer of this type of collaborative arrangement. We hope that our colleagues from Australia will carry back that message after this workshop.

In conclusion, let me again extend a warm welcome to visitors from ICAR, ACIAR, and QDPI. I wish the workshop well and I look forward to seeing the published report.

J.G. Ryan
Director General
ICRISAT
Andhra Pradesh
India

Cooperation between ICAR and ACIAR

I am very happy to be associated with this important workshop on groundnut. It gives me immense pleasure to know that novel research will be taking place in the area of water-use efficiency (WUE) in groundnut under the ACIAR–ICAR–ICRISAT collaborative project.

When we look at the historical evolution of groundnut, I feel that the crop was not selected for adaptation to drought. Except for some parts in South America such as Brazil, where it is subjected to drought, the groundnut is not exposed to the kind of drought that occurs in our agroecological situation, particularly in Africa and India. In India, Gujarat and Andhra Pradesh represent two typical agroecological zones where drought severely constrains productivity. In view of the situation there is an urgent need to stabilise yields of groundnut in these drought-prone environments. Unlike other crops, groundnut is subject to drought not only at the level of root system but also at gynophore level, which can make the situation all the more complicated.

Although many data have been generated on the performance of groundnut under drought conditions in India, they have not been fully utilised. This situation has occurred because much of the drought research has not been given proper direction and guidance. Several varieties have been screened and found to be tolerant to drought, but the work has not been followed up.

In this context it is very gratifying to see the collaborative project between ACIAR, ICAR and ICRISAT to address the WUE problem. To give a brief account of the evolution of this collaborative project, I recall that we had a meeting with Drs Peter Smith and Graeme Wright in April 1991, and that subsequently the ACIAR project coordinator (groundnut) became involved. Collaborating centres representing a wide range of environments in which groundnut is grown in India were identified. We identified Tirupati, Vridhachalam, Junagadh, Jalgaon and Durgapura as potential collaborators. In addition to these, we have identified the University of Agricultural Sciences, Bangalore as a special centre to conduct basic research on WUE of selected legume crops. I am sure that this workshop on methodology will be relevant and productive.

The collaboration between Australia and India is not new. We have had collaborative links with Australia in a wide range of fields. For example, we have had collaborative projects on arid-zone research, involving the Central Institute for Arid-zone Research at Jodhpur, and on wheat rust, involving Dr I.A. Watson, over a considerable period of time.

I am sure that my colleagues in ICAR, particularly in AICORPO, are very interested in, and committed to, this collaborative project. I am sure the project will commence with the supply of some basic infrastructural facilities required in drought research which will put the research on a very sound footing.

I would like to thank Dr Ryan and Dr McDonald for arranging this meeting at ICRISAT. I thank the organisers of the workshop for giving me the opportunity to speak and I wish the workshop success.

M.V.R. Prasad
Director
Directorate for Oilseeds, ICAR
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India

Brief Overview of ACIAR Activities

THIS is my first visit to India and ICRISAT, and I am grateful for the warm welcome I have received. I did spend about six years working on agronomy of forages and pastures in Indonesia, where there are problems similar to those in India. The semi-arid tropics (SAT) represent a vast area across the world, and the topic we are discussing in this workshop is very relevant to this large area, where help is urgently needed to increase and stabilise food production.

As you know, ACIAR is a part of the Australian development assistance program, and particularly promotes and facilitates research and development between Australian and overseas research groups. ACIAR does not do the research itself. Rather we commission groups within Australia, the Queensland Department of Primary Industries for example, to undertake research on its behalf in conjunction with research groups in overseas countries.

A very strong requirement for any ACIAR project is that there are joint benefits for Australia and overseas countries. These benefits usually come from technologies which improve agricultural production and through research resource and staff development, both in Australia and overseas.

ACIAR has programs in many different areas of agriculture, with crops being one of them. There are eight other programs, on aspects such as livestock, fisheries, forestry, postharvest technology, land and water resources and farming systems. Each of this programs is lead by research program coordinator (RPC).

ACIAR has a annual budget of about $Au30 million (about 750 million rupees), and has around 100 research projects going at any one time. So, each project may receive about $150–250000 per year. The funding goes to research groups in Australia and overseas.

New projects commence with identification of problems common to Australia and an overseas developing country. The identification of a problem may come from several different sources, e.g. from a research group in Australia or in a developing country, or directly from an ACIAR RPC. Often the projects are built on earlier work, as is the case in the project we are meeting here to discuss. The development of a project then involves the preparation of a detailed research plan, which should include the range of activities to be conducted, performance indicators and details of project progress reviews to be undertaken. These are the issues we will be clarifying at this WUE project workshop, including the technologies and methodologies to be used across different sites, and the ways in which the project results will be reviewed.

The current project is an excellent one with very relevant groups involved. I am certainly very pleased to be involved at the start of it. It is a project dealing with a serious problem and the groups involved — QDPI, ANU, ICAR, ICRISAT and UASB — all have very good expertise in drought and WUE research.

Dr M.V.R. Prasad mentioned before the similarities between ACIAR and ICAR. I am very impressed with the way in which agricultural R and D is coordinated across states in India. It involves all the national programs going across all states, and is something which we in Australia have not yet developed. I am sure Australia can learn a lot from India concerning the coordination of agricultural research.

The groundnut crop is very important in India as well as in Australia. In the SAT, WUE is one of the high priority areas for this crop. There is a very impressive new technique, as Dr Ryan mentioned, to help with assessing the world's groundnut germplasm for WUE. I think this project has great potential for progress. I would like to pay tribute to Dr Peter Smith, the previous RPC (Crops) in ACIAR, and also to Drs G.C. Wright, R.C. Nageswara Rao and M.S. Basu, who were all instrumental in developing this project.

I look forward to participating in this workshop.

Colin Piggin
Research Program Coordinator
Crop Sciences
ACIAR

Water-use Efficiency and Drought

Introduction to 'Selection for Water-use Efficiency in Food Legumes': Project Background, Objectives and Outputs, and Scope of Workshop

G.C. Wright*

Background

A previous ACIAR-funded project on peanut improvement in Indonesia (Project No. 8834: 1986–1991) investigated constraints to groundnut productivity in both Indonesia and Australia. The project investigated pathological, agronomic and ecophysiological factors which limit groundnut productivity, and proposed new practices and potential solutions to overcome many of these limits (see Wright and Middleton 1992).

Drought was identified as a major limit to groundnut productivity in many regions, particularly as groundnut is largely grown as a rainfed crop in many cropping systems. The groundnut improvement project investigated both management and genetic options available for ameliorating the effects of drought. Management strategies such as supplementary irrigation and choice of appropriate plant populations were shown to improve groundnut yields under particular drought regimes. The genetic solution, via selection and breeding of plants that can tolerate or avoid severe water deficits, however, is one of the few low-cost avenues available for improving groundnut productivity in the long term.

The traditional approach to breeding cultivars with superior yield performance under water-limited conditions has been empirical, via selection for yield under stress conditions. Such a task is both prolonged and expensive, requiring massive plant populations. Plant breeders and crop physiologists now believe more rapid progress can be aided by a priori knowledge of the physiological basis of crop performance under drought conditions (e.g. Shorter et al. 1991; Williams and Saxena 1991). This strategy involves the breeding of better adapted and higher yielding cultivars by identifying reliable traits of drought tolerance to complement conventional breeding programs.

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Passioura (1986) suggested that for a trait to be useful it must benefit one of the main functional components in the following biological model for seed yields:

$$\text{Seed yield} = \underset{(T)}{\text{Water transpired}} \times \underset{(WUE)}{\text{Water-use efficiency}} \times \underset{(HI)}{\text{Harvest index}}$$

Figure 1 illustrates how these three parameters can interact to determine final pod yield. Project No. 8834 analysed cultivar variation in yield performance in terms of the above biological model and concluded there was substantial genetic variation in each of the functional components contributing to seed yield in groundnut. Specifically, it demonstrated that highly significant variation in water-use efficiency (WUE), defined as total biomass production per unit of water transpired (g/kg), exists among cultivars of groundnut. This research, in combination with work on other crops in the ACIAR-funded project (Project No. 8550) on legume WUE, has overturned the widely accepted belief that there was no intra-species variation in WUE (e.g. Tanner and Sinclair 1983).

The difficulty in accurately measuring WUE in either glasshouse or field conditions means it is virtually impossible to include such a trait in breeding programs. However, research in the abovementioned projects has demonstrated that leaf carbon isotopic composition (Δ) is well correlated with WUE, and raised the possibility of using Δ as a rapid, non-destructive and relatively inexpensive technique for selection of WUE in groundnut breeding programs. It was also shown that specific leaf area (SLA, cm^2/g), or 'leaf thickness', was extremely well correlated with WUE over a wide range of cultivars and environments. This observation highlighted the possibility of using SLA as an even more rapid and inexpensive technique for selection of WUE. This finding has significant implications for groundnut breeding

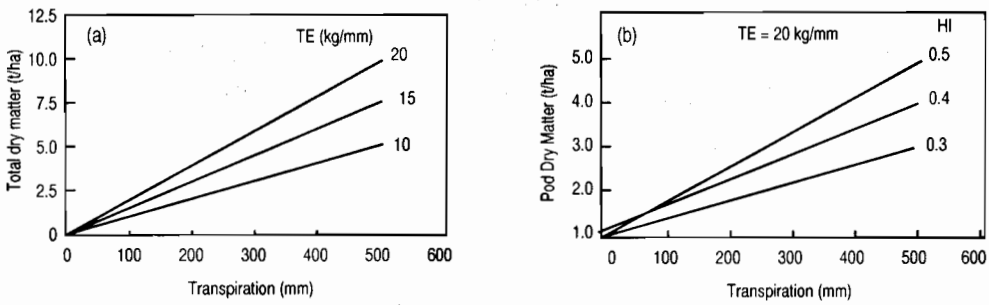

Fig. 1. Relationship between transpiration and total dry matter with (a) varying levels of transpiration efficiency (TE), and (b) the relationship between transpiration and pod dry matter with varying harvest index (HI).

programs in developing countries where access to mass spectrometer facilities to measure Δ is limited.

Studies on WUE variation in some of the other important food legumes grown in India and Australia are not as far advanced as for groundnut. Although there have been preliminary glasshouse studies into WUE variation (and correlation with Δ) in cowpea (Ismail and Hall 1992) and navybeans (Ehleringer et al. 1991) there are no published data available for soybean and chickpea. There is therefore a need to assess the extent of cultivar variation in WUE, and correlation with Δ and/or SLA in these crops under both glasshouse and field conditions. Also, the existence of possible negative associations between WUE and HI (or T) needs to be thoroughly studied before WUE, Δ and SLA can be recommended as suitable traits for selection in the breeding programs.

Following the ACIAR independent review of the project on peanut improvement in Indonesia, it was recommended that the drought physiological research should be continued as a new project, focusing on selection for WUE in groundnut and some other food legume breeding programs. As India is the world's largest producer of groundnuts, and drought severely limits productivity of this and other crops, it was considered India was an appropriate country in which to conduct this collaborative research project.

Project Objectives and Expected Outputs

Project No. 9216 has the following objectives.

- To identify and select in India groundnut cultivars with high WUE and partitioning characteristics from the world germplasm collection and genetic material from applied groundnut breeding programs.
- To evaluate the yield performances of these parent lines or progenies in appropriate target environments in India.
- To determine the extent of cultivar variation in WUE, and its correlation with Δ, HI, and the relationship of these traits to seed yield in soybean, cowpea, chickpea and navybean.

The following outputs are expected.

- Groundnut cultivars with high WUE and HI, which have been shown to have high yield potential under water-limited conditions in the semi-arid tropics.
- Establishment and demonstration of sound screening methods for high WUE, based on either Δ or SLA, for breeding programs in India, Australia and other countries producing rainfed groundnuts.
- Demonstration that simple and easily measured physiological traits, such as Δ or SLA, can be used to enhance the rate of yield improvement in groundnut breeding programs by improving the efficiency of selection and increasing genetic diversity.
- Assessment of the extent of cultivar variation in WUE in other food legumes, and the potential for incorporation of simple selection criteria such as Δ or SLA in breeding programs aimed at improving the drought tolerance of these crops.
- Training of Indian scientists in glasshouse and field techniques for WUE measurement, to improve the efficiency of current breeding programs aimed at improving the drought tolerance of food legumes.

- Documentation and publication — in appropriate national and international newsletters and journals — of the results from the research program

Scope of Workshop

The main aims of this workshop are to:

- establish the extent to which drought constrains groundnut productivity in various regions of India, and describe the nature of past and current research aimed at alleviating its impact on yield;
- provide collaborating scientists with a background knowledge of recent WUE research, as a prelude to the proposed research project on selection for WUE in food legumes;
- describe the objectives, proposed workplan and expected outcomes of the project;
- develop standardised experimental workplans and techniques for use in the multi-location trials involving assessment of selected high WUE and high partitioning lines under different drought regimes;
- allow all participants to meet and interact in developing meaningful and workable experimental plans to achieve the project objectives.

References

Ehleringer, J.R., Klasen, S., Clayton, C., Sherill, D., Fuller-Holbrook, M., Fu, Q. and Cooper, T.A. 1991. Carbon isotope discrimination and transpiration efficiency in common bean. Crop Science, 31, 1611–1615.

Ismail, A.M. and Hall, A.E. 1992. Correlation between water-use efficiency and carbon isotope discrimination in diverse cowpea genotypes and isogenic lines. Crop Science, 32, 7–12.

Passioura, J.B. 1986. Resistance to drought and salinity: avenues for improvement. Australian Journal of Plant Physiology, 13, 191–201.

Shorter, R., Lawn, R.J. and Hammer, G.L. 1991. Improving genotypic adaptation in crops — a role for breeders, physiologists and modellers. Experimental Agriculture, 27, 155–175.

Tanner, C.B. and Sinclair, T.R. 1983. Efficient water use in crop production: research or re-search? In: Taylor, H.M., Jordan, E.R. and Sinclair, T.R., ed., Limitations to efficient water use in crop production. American Society of Agronomy, Crop Science Society of America and Soil Science Society of America, 1–27.

Williams, J.H. and Saxena, N.C. 1991. The use of non-destructive measurement and physiological models of yield determination to investigate factors determining differences in seed yield between genotypes of desi chickpeas (*Cicer arietum*). Annals of Applied Biology, 119, 105–112.

Wright, G.C. and Middleton, K.J., ed. 1992. Peanut improvement: a case study in Indonesia. ACIAR Proceedings No. 40.

Importance of Drought Stress and Its Alleviation in Legumes

C. Johansen and S.N. Nigam*

AMONG biotic and abiotic stresses constraining yield of rainfed grain legumes, drought stress ranks high on a global basis. As part of ICRISAT's medium-term planning for the period 1994–98, we have tried to quantify yield losses attributable to drought for the ICRISAT mandate legumes — groundnut, chickpea and pigeonpea — in their major growing regions across the world. A first step was to identify research domains within which major yield constraints were similar and amenable to an integrated research effort to alleviate them. Mean yields recorded in each domain were taken as a baseline against which projected improvements to ameliorate specific constraints could be measured. Table 1 gives the situation in India.

Yield losses attributable to moisture deficit, estimated by differences between rainfed and irrigated yields recorded across the domain, were calculated in terms of total production loss and value of that loss on the basis of current prices (Table 2). Estimates were made of the extent to which such losses could be retrieved by genetic improvement (Tables 1 and 2). However, it was necessary to discount the value of such gains by taking into account factors such as probability of success of the intended research and development effort, the expected ceiling rate of adoption and time lags anticipated in the research and adoption process (Table 2). Benefit:cost ratios could then be calculated to indicate the returns on investment expected for genetic improvement to alleviate drought constraints for each crop (Table 2). These data were used to prioritise research themes for the Institute across crops and disciplines (Table 2). Before doing this, however, benefit:cost ratios were weighted to take account of equity (to what extent improvements will assist marginal farmers), internationality (spillover effects of successful research) and sustainability (environmental effects).

There are many possible routes by which genetic improvements may lead to higher yielding grain legumes under drought limitations. A summary of these drought adaptations amenable to favourable genetic manipulation follows. The terms used are explained in detail in Ludlow and Muchow (1990). The items marked with an asterix can make a direct contribution to water-use efficiency (WUE).

Table 1. Average yield (t/ha) of groundnut, chickpea and pigeonpea in farmers' fields in various states of India and percentage increase in yield expected through a concerted research effort to improve genetic adaption to drought.

Research domain	Representative Indian State	Farmers' field yield (t/ha)	Expected yield increase through genetic improvement (%)
Groundnut			
I	Gujarat	0.5	10
II	Madhya Pradesh	0.7	6
III	Orissa	0.75	3
IV	Andhra Pradesh	0.7	10
Chickpea			
I	Maharashtra	0.5	30
II	Madhya Pradesh	0.7	25
III	Haryana	0.8	20
IV	Uttar Pradesh	0.9	10
Pigeonpea			
I	Haryana	0.9	20 (10)[a]
II	Bihar	1.2	20 (5)
III	Maharashtra	0.7	25 (7)
IV	Andhra Pradesh	0.2	100 (20)

[a] Values in parentheses represent expected yield increase if other major constraints, such as pests and diseases, were not alleviated.

A. Drought escape

1. Early maturity
2. Phenological adjustment

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Table 2. Estimated annual value (US$m) of yield loss, potential yield gain, net present value of successful research and benefit:cost ratio for genetic improvement to alleviate drought, measured across all domains.

Crop	Yield loss (US$m)	Potential yield gain (US$m)	Net present value (US$m)[a]	Benefit: cost ratio	Research theme ranking[b]
Groundnut	520	208	14.5	5.2	19
Chickpea	1058	525	265.2	113.2	3
Pigeonpea	570	92	19.7	7.7	47

[a] Calculated considering probability of success, ceiling rates of adoption and time value (discounted cash flow) relating to anticipated research and adoption lags.
[b] Out of 92 themes proposed for core funding
Source: ICRISAT Medium Term Plan 1994–98, Volume 1. Main Report.

B. Dehydration avoidance
1. Root attributes
   a. Rooting depth
   b. Root length density
   c. Root hydraulic conductivity*
2. Shoot attributes
   a. Canopy structure*
   b. Leaf movements*
   c. Leaf reflectance and other surface characteristics*
   d. Stomatal control*

C. Dehydration tolerance*
1. Metabolism at reduced water potential
2. Low lethal water status
3. Osmotic adjustment
   a. Root tissue
   b. Shoot tissue

D. Heat tolerance*

E. Integrated traits assisting crop performance
1. Seedling establishment
   a. Germination at low soil-water potential
   b. Seedling emergence and survival at low soil-water potential
2. Early growth vigour
   a. Roots
   b. Shoots
3. Leaf area maintenance
4. WUE
5. Developmental plasticity
   a. Adjustment of phenology to intermittent stress pattern
   b. Recovery
   c. Remobilisation of pre-anthesis assimilates

For all three of the ICRISAT mandate legumes, exploitation of drought escape (through widespread adoption of newly bred shorter duration cultivars and those in the breeding pipeline) offers the greatest scope for improving yields in drought-prone environments with a short growing season. Other traits amenable to exploitation exist at different levels of complexity (or organisation). WUE is an integration of several possible processes that can operate, but is still only one of many options for alleviating drought stress in these legumes. In the course of this particular WUE project, the relative merits of WUE vis-à-vis other options need to be kept in mind. As research proceeds, the projections indicated in Tables 1 and 2 will undoubtedly need adjustment, and participants are encouraged to assemble the data needed to do this.

Identification of traits contributing to drought resistance in the target legumes, and assessment of the magnitudes of any benefits expected, are only first steps in the development of truly drought-resistant cultivars. During this project, the following considerations must be borne in mind:

- are our target drought environments adequately defined, so that appropriate groundnut ideotypes are being developed?
- are we dealing with easily detectable traits, readily recognisable in segregating populations?
- what breeding methodology should be followed to best ensure incorporation of drought-resistance traits into an otherwise desirable cultivar background?
- what is the appropriate selection environment for each generation of the drought breeding program?

- what trade-off of other desirable traits (e.g. yield potential) is necessary in order to improve drought resistance?
- what degree and type of multilocation testing is needed to ensure that selections from a drought-breeding program are indeed superior for a given drought-prone region?

Even having completed a drought-breeding exercise, and demonstrated genetic gain in drought environments, the question of how to transfer the benefits to farmers' fields also needs to be addressed. Those involved in basic research need to become involved in this activity if they wish to see the fruits of their efforts. Thus, from an early stage in the research process, we must continually question the level of improvements in drought resistance needed to interest to both resource-poor and better-endowed farmers. We should also be concerned with the extension and seed-production capabilities available for the target regions to facilitate adoption of improved cultivars.

Finally, it is strongly recommended that this project establish links with the 'Global grain legumes drought research network' (GGLDRN), a recent initiative of ICRISAT and ICARDA. This will enhance contact with other such projects on improvement of drought resistance in grain legumes being carried out elsewhere, and permit rapid dissemination of the findings of this project. The twice-yearly publication of the network newsletter, *News and Views of GGLDRN*, can have an important role in this regard.

Reference

Ludlow, M.M. and Muchow, R.C. 1990. A critical evaluation of traits for improving crop yields in water-limited environments. Advances in Agronomy, 43, 107–153.

Drought Patterns and Drought Research Activities at Collaborating Institutions in India

Drought Research on Groundnut Under the All India Coordinated Project

M.S. Basu*

INDIA is endowed with diverse agroclimatic conditions, enabling the growth of a wide range of oilseeds. Of the nine cultivated annual oilseeds, namely castor, groundnut, linseed, rapeseed and mustard, safflower, sesame, soybean, sunflower and niger, groundnut occupies 34.5% of the total oilseeds area (24 million ha) and 41.3% of the total oilseeds production (18.5 million t). India is the world's largest producer of groundnuts.

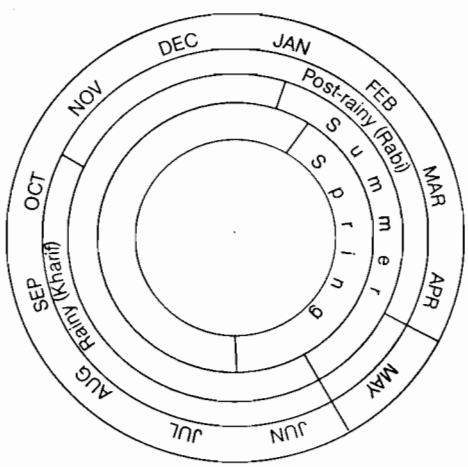

Figure 1. Groundnut cropping season in India

Growing season: In India, groundnut is grown in four seasons: rainy (80% of total area), post-rainy (15%), summer (5%) and spring (negligible, Fig. 1). Groundnut produced in the rainy season during the southwest monsoon period (June–November) is spread over the entire country and is usually rainfed. The post-rainy season crop is confined to southern and southeastern areas of India, and is largely grown in rice-fallows with residual moisture and limited irrigation during October–March. The summer crop is restricted to the central, western and northern states and is grown during January–May under irrigation. Spring groundnut is grown after harvest of potato and toria in northern and eastern states during February–June under irrigated conditions.

Production and productivity: Despite the fact that India is the largest producer of groundnuts in the world, its productivity (783 kg/ha) is much lower than the world average of 1148 kg/ha (FAO 1991: Table 1). This low productivity occurs under a largely rainfed production system, where several biotic and abiotic stresses limit yield. The major yield constraints are pests and diseases, and unreliable rainfall resulting in drought. Depending on the severity of drought, pod yield varies from 550–1100 kg/ha (Fig. 2), and consequently the total annual production varies between 4.3 and 9.6 million t. This seasonal and spatial variability in yield creates major problems for India.

Table 1. World groundnut statistics, 1991

Country	Area (million ha)	Production (million t)	Productivity (kg/ha)
World	20.36	23.37	1148
Asia	13.11	15.22	1161
India	8.26	7.00	847
China	3.05	6.06	1984
N. America	1.00	2.46	2461
USA	0.81	2.24	2760
Africa	5.82	4.92	846
Developed (all)	0.96	2.48	2589
Developing (all)	19.40	20.89	1077
India's contribution	40.6%	30%	

* National Research Centre for Groundnut (ICAR), Gujarat, India

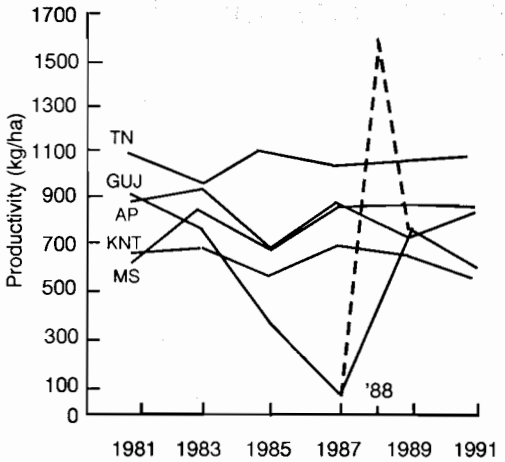

Figure 2. Trend in productivity of rainy season groundnut in major states in India: TN, Tamil Nadu; GUJ, Gujarat; AP, Andhra Pradesh; KNT, Karnataka; MS, Maharashtra

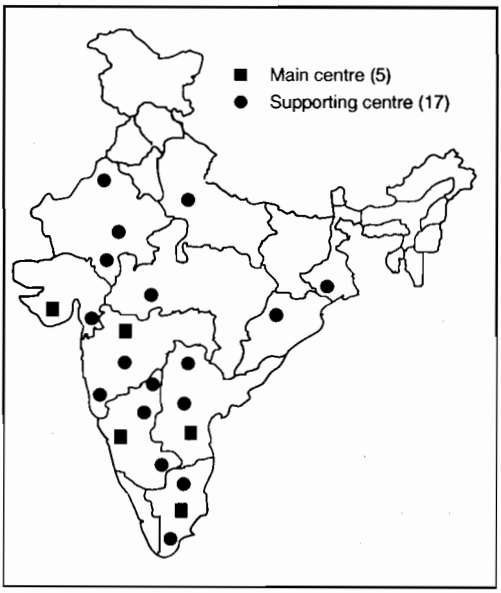

Figure 3. All India Coordinated Project groundnut research centres

Research

Biotic stresses

Under the All India Coordinated Research Project on Oilseeds (AICORPO), the breeding of groundnut varieties resistant/tolerant to biotic and abiotic constraints is the number one priority. Multidisciplinary research is conducted at 5 main and 17 supporting centres located in major groundnut growing states in the country (Fig. 3). Some of the significant achievements to date have been the development of foliar-disease-resistant varieties such as Girnar 1, ICG (FDRS) 10, ICGV 86590 for southern India, where these diseases are serious.

Abiotic stresses

Among the several abiotic stress factors, drought is most the important. Yields are low in semiarid tropical (SAT) regions, which are characterised by a highly variable rainfall. In India, rainfall varies from 500 mm (Rajasthan) to 4000 mm (Assam) and large variations exist not only between but also within seasons. The percentage deviation of annual rainfall from the mean in the Anantapur district of Andhra Pradesh (the largest groundnut growing district in the world at 0.5 million ha) is depicted in Figure 4, which shows how the crop has to cope with poor rainfall distribution. Scanty rainfall areas are usually associated with high rainfall coefficient of variation (CV). In major groundnut growing states of India, CVs vary from 40 to 80%. The CV of rainfall in humid climates is about 10–20% whereas in SAT climates it is around 20–30%. In extreme cases CVs as high as 60–80% have been recorded in Rajasthan, and 40–50% in the Sourashtra region of Gujarat.

Apart from total crop failure, drought periods of varying duration occur during the rainy season in the major groundnut areas and adversely affect pod yields. These areas include the Rayalseema region of Andhra Pradesh, the Sourashtra region of Gujarat and Vidharva, and the Marathawada region of Maharashtra. The groundnut centres under AICORPO have been classified as early, mid and terminal drought areas, depending on the timing of water stress in relation to crop growth.

Drought research

Current research on drought under AICORPO is confined mainly to the identification of resistant/tolerant genotypes through screening, at national/international drought nurseries at multi-location sites. In the absence of specific parameter(s), selection has been based on pod yield/dry matter production, or harvest index, under natural drought conditions. Experiments on drought responses

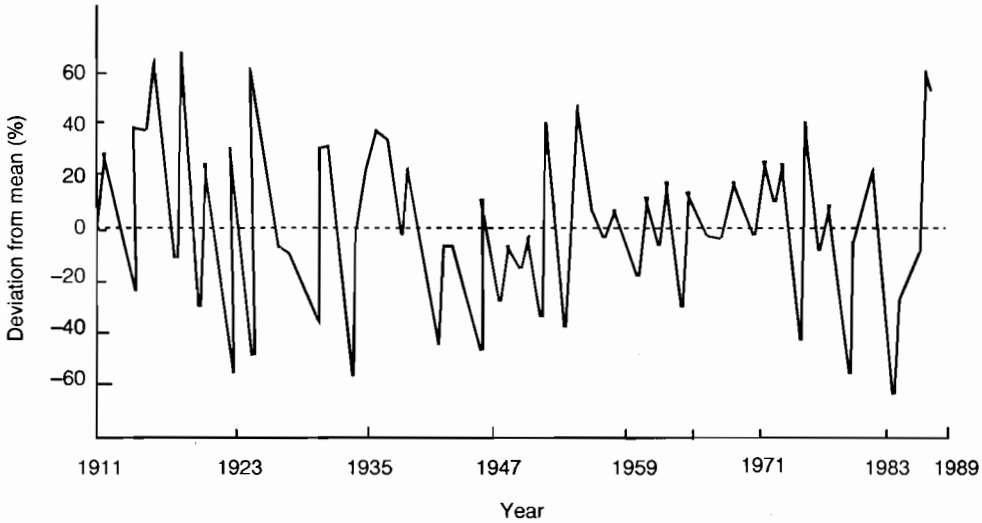

Figure 4. Percentage deviation from mean of annual rainfall at Anantapur, 1911–1989

under simulated drought conditions are in progress in some centres. Results obtained to date indicate responsiveness to selection during the different drought phases. Genotypes identified as tolerant to different phenophases are:

- Early-drought phase (at Vriddhachalam and Tindivanam): Sel. 13, F 1–5, JL 24, ICGVs 86744, 86610, 86187, 87354, ICG 3505, 3556, 3736, Ah 817/S.
- Mid-drought phase (at Durgapura GAU and NRCG): ICGVs 87118, 87354, 86169, 86187, ICG 3143, 3505, 3556.
- End-drought phase (at Junagadh and Durgapura): ICGs 4581, 3400, 3143, ICGVs 8604, 86610, 86744, 86200, 86647, 86187, 87354.

Interestingly, some of the lines were found to be tolerant to drought across the locations over a number of years. These are:

ICG 3505	:	at 5 locations for 2 years
ICG 3736	:	at 3 locations for 2 years
ICG 3400	:	at 4 locations for 2 years
ICGV 87354	:	at 9 locations for 3 years
ICGV 86187	:	at 4 locations for 2 years
ICGV 86647	:	at 4 locations for 2 years

Some of the advanced breeding lines showing good yield potential (namely TVG 4, TVG 5, ICGV 87354 and ICGV 87357) will now be tested in large plots at selected locations where drought is a common feature. The germplasm lines identified as tolerant can be utilised as parents in breeding varieties tolerant to drought.

Future program

Groundnut drought research in India is being strengthened at six locations (Durgapura, Junagadh, Jalgaon, Tirupati, Vriddhachalam and Bangalore) under the ACIAR–ICAR–ICRISAT collaborative project on WUE.

This workshop will address relevant methodologies and operational aspects, and formulate detailed work plans to examine genotypic variation in the efficiency of water use in groundnut germplasm under a wide range of drought conditions.

Drought Research on Groundnut at ICRISAT Centre

R.C. Nageswara Rao*

DROUGHT research on groundnut conducted at ICRISAT Centre (IC) over the past decade can be grouped into three broad areas: screening and evaluation of genotypes for drought tolerance; strategic research on physiological mechanisms; and some applied research on drought management. Due to limitations of time, I wish to concentrate on progress made in the first two areas, which are relevant to the present workshop. Drought research in groundnut at IC began in 1980, with experiments to examine the timing of irrigation and plant population. Screening of genotypes for drought tolerance began after the 1981–82 post-rainy season.

Screening of Genotypes for Drought Tolerance

Drought is a complex syndrome involving three main factors — timing, intensity and durations — all of which vary widely in nature. The extreme variability in these environmental components between years and sites has made it difficult to define plant attributes required for improved performance under all drought situations. Selections of drought tolerant genotypes can be made by testing large numbers of genotypes in multiple seasons and locations, but this, together with selection procedures based on yield measurements at harvest, will be costly in terms of time and space. Therefore, in the long run, reliable indices for drought tolerance are needed to complement conventional improvement programs.

Philosophy

We adopted a holistic approach in selecting genotypes with drought tolerance. Initially, genotypes are evaluated on the basis of yield and total dry matter produced under simulated drought conditions in the field. The basic advantage in this approach is that the selection criteria integrate all the additive effects of many underlying mechanisms of drought tolerance. Secondly, the material identified as drought tolerant/susceptible is then examined for the physiological basis of genotypic differences in yield under drought conditions so as to identify physiological attribute(s) contributing to drought tolerance. It is recognised that this knowledge on physiological mechanisms can improve existing screening methods or permit development of new ones. The screening for single attributes is important, we believe, for the selection of complementary parents which may have different reasons for drought tolerance.

Screening Methodology

Drought screening experiments at IC are conducted mainly during the post-rainy season (Nov–Apr) to avoid interference from rains. In the early studies we investigated genotypic sensitivity to various patterns of drought (single and multiple droughts) and its relationship with yield potential (yield under non-stress conditions) in a range of groundnut genotypes. These results have shown that when water deficit occurred at seedfilling phase genotypic yield potential accounted for about 90% of the variations in pod yield sensitivity to drought (Nageswara Rao et al. 1989), suggesting lack of scope for combining yield potential with low sensitivity to acute droughts spanning seed-filling phase. However, pod yield potential accounted for less of the variation in drought sensitivity (15–60%) in early and mid-season drought, suggesting that for mid-season droughts it may be possible to identify genotypes with both high yield potential and relatively low sensitivity to drought. Currently, genotypes are screened for the two most predominant droughts, i.e., mid-season and terminal drought. A range of water deficits is created within a given drought treatment, using a line-source sprinkler system (Hanks et al. 1976). Genotypes are evaluated on the basis

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of total dry matter and pod yield produced across a range of water deficits relative to the mean of all entries in the experiment. (Nageswara Rao 1991; Singh et al. 1991).

Under mid-season drought conditions, recovery of growth when water becomes available plays an important role. Significant genotypic differences in rate of recovery from mid-season drought were found (Harris et al. 1988). Numbers of genotypes screened for drought tolerance at IC since 1981 are given in Table 1.

As a part of screening methodology, selected genotypes are further evaluated for their performance under rainfed conditions in drought-prone regions such as Anantapur in Andhra Pradesh, and through national and international drought nurseries conducted in collaboration with various national research systems (NARS) (Table 2). This activity enabled NARS to participate in screening, and to identify material suitable for a given region. In the national drought nursery conducted by the All India Coordinated Research Project on Oilseeds (AICORPO) during the 1988–1990 rainy seasons in India, five genotypes were identified as being superior to local checks in performance (18–30%) under drought conditions. The flow of material through the screening process is indicated in Figure 1.

Strategic Research

Strategic research on drought in groundnut has been conducted in close collaboration with national and international institutions (Table 3). We examined the physiological basis of genotypic difference in yields under water deficit conditions, based on a central relation which has been applied to many arable crops:

$$Y = T \times \text{WUE} \times p$$

where pod yield (Y) can be expressed as the product of the total amount of water lost by transpiration (T), dry matter: water-use ratio (WUE), and ratio of pod yield to total dry matter (p). Significant variability among genotypes has been found for all the three parameters (Mathews et al. 1988; ICRISAT 1990; Nageswara Rao et al. 1993), which suggested scope for selection of genotypes based on single attributes. However, accurate measurement of T, WUE and p in the field is a difficult task.

Table 1. Number of genotypes screened for drought tolerance at IC since 1981

Year (post–rainy season)	Genotypes screened[a]	New material from:		Carryover from:	
		breeding lines	germplasm accessions	breeding lines	germplasm accessions
1981–82	EB 200	9	191	–	–
1982–83	EB 242	63	111	8	60
1983–84	EB 477	295	182	–	–
1984–85	EB 128	–	10	56	62
1985–86	–	–	–	–	–
1986–87	144	135	–	2	7
1987–88	EB 124	29	62	29	4
	VB 20	20	–	–	–
1988–89	EB 291	29	62	29	4
	VB 100	83	9	6	2
1989–90	EB 432	264	86	51	31
	VB 261	229	25	5	2
1990–91	EB 49	48	–	–	1
	VB 25	24	–	–	1
1991–92	EB 181	155	–	22	4
	VB 81	80	–	–	1
1992–93	EB 173	119	49	2	3
	VB 92	85	29	8	–
Total	3020	1764	810	220	226

[a] EB = spanish and valentia types; VB = virginia bunch types.

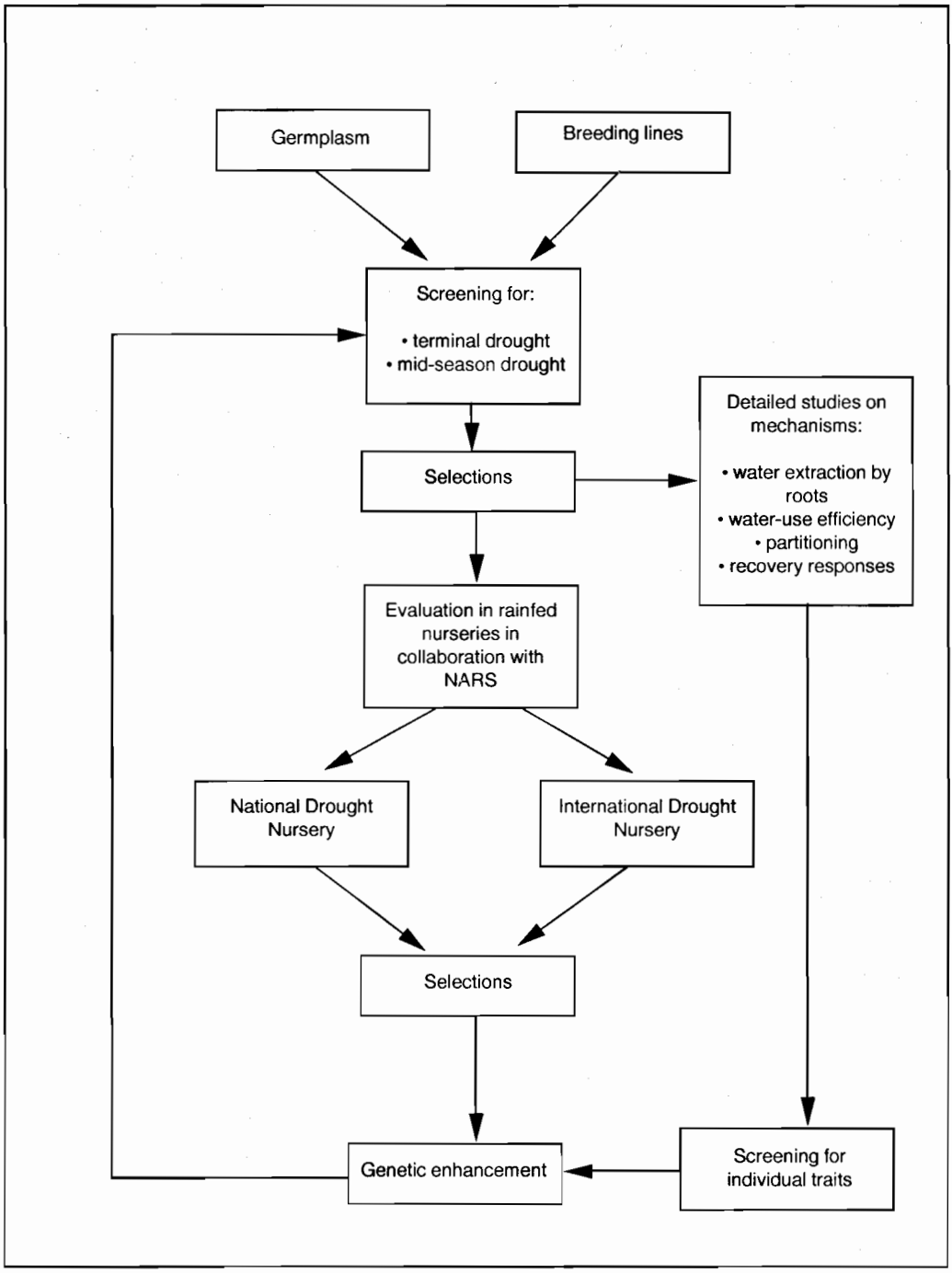

Figure 1. Flow of groundnut genotypes in drought screening program at ICRISAT

Table 2. List of national and international drought nurseries sent to various countries

Year	No. of drought nursery sets supplied		
	National	International	Countries
1988	6 sets (18 entries)	–	
1989	6 sets (18 entries)	4	Indonesia, Thailand, Philippines, India
1990	6 sets (22 entries)	2	Indonesia, India
1991	6 sets (22 entries)	10	Bangladesh, China, Honduras, Saudi Arabia, Sierre Leone, Thailand, Vietnam
1992	6 sets (22 entries)	15	Bangladesh, Brazil, Ethiopia, India, Indonesia, Mali, Nigeria, Republic of Yemen, Sudan, Vietnam

A close positive relationship between dry matter production and transpiration in groundnut genotypes (Azam-ali et al. 1989) suggested that productivity cannot be enhanced by limiting the transpiration whereas any genetic trait(s) or management practice(s) enhancing T can improve productivity. Studies conducted with a limited number of genotypes indicated significant variability in root characteristics and the ability of roots to extract water from deeper soil profile (Watterott 1991; ICRISAT 1990; Wright et al. 1993). However, we need to know more about the extent of variation in roots, and the benefits or penalties associated with selection for root characteristics in groundnut.

Significant variation among groundnut genotypes for WUE (defined as g dry matter produced per kg of water transpired) under field conditions has been observed (Mathews et al. 1988). Close collaboration between ICRISAT and ACIAR in the past few years, in studies on the groundnut drought physiology, has resulted in very productive research in WUE (Wright et al. 1993, 1994; Nageswara Rao and Wright 1994). These significant findings formed the basis for the enhanced cooperation between ICRISAT, ACIAR and ICAR in WUE research.

Table 3. National and international cooperation in drought research on groundnut at ICRISAT

Year	Lead cooperator(s)	Research area
1981–85	Dr J.L. Monteith et al. Univ. of Nottingham, U.K. (ODA-funded project)	Physiological basis of drought tolerance
1986–87	Dr F. Lenz et al. Univ. of Bonn. (GTZ-funded project)	Root studies in drought tolerant and susceptible genotypes
1986–Cont	Dr M. Udaykumar et al. University of Agricultural Sciences (ICRISAT–ICAR collaborative project)	Basic studies on drought tolerance traits
1988–Cont	AICORPO[a] (ICRISAT–ICAR collaborative project).	National Drought Nursery of groundnut
1989–Cont	Dr G.C. Wright, QDPI, Kingaroy Dr G.D. Farquhar, Australian National University, Canberra (ICRISAT–ACIAR collaborative project)	Water-use efficiency and carbon isotope discrimination

[a] All India Coordinated Research Project on Oil seeds.

The physiological basis for genotypic differences in recovery responses (after release of mid-season drought) is being examined in collaboration with the University of Agricultural Sciences, Bangalore. The results available so far indicate that reproductive development during recovery period seems to be related to cytokinin flux from the root systems. The role of hormones in general, and cytokinin in particular, on reproductive development and partitioning of dry matter to pods, requires further research.

Future Plans

- Screening of germplasm and breeding lines for drought tolerance at IC, and evaluation of selected lines through nurseries will continue. Novel methods will be used to identify genotypes with greater WUE and partitioning.
- Research on genotype × environment interactions for WUE will continue in collaboration with ACIAR and ICAR through the present collaborative arrangement.
- Research on the role of hormones in reproductive growth during recovery from mid-season drought will continue in collaboration with the University of Agricultural Sciences, Bangalore.
- Strategic research on high-temperature tolerance will be initiated.

References

Azam Ali, S.N., Simmonds, L.P., Nageswara Rao, R.C. and Williams, J.H. 1989. Population, growth and water use of groundnut maintained on stored water. III. Drymatter, water use and light interception. Experimental Agriculture, 25, 77–86.

Hanks, R.J., Keller, J., Rasmussen, V.P. and Wilson, G.D. 1976. Line-source sprinkler for continuous variable irrigation crop production studies. Soil Science Society of America Journal, 40, 426–429.

Harris, D., Mathews, R.B., Nageswara Rao, R.C. and Williams, J.H. 1988. The physiological basis for yield differences between four groundnut genotypes in response to drought. III. Development processes. Experimental Agriculture, 24, 215–226.

ICRISAT (International Crops Research Institute for the Semi-arid Tropics) 1990. Annual Report 1989. Patancheru, A.P. 502 324, India, ICRISAT, 143.

Mathews, R.B., Harris, D., Nageswara Rao, R.C. and Williams, J.H. and Wadia, K.D.R. 1988. The physiological basis for yield differences between four groundnut genotypes in response to drought. I. Dry matter production and water use. Experimental Agriculture, 24, 191–202.

Nageswara Rao, R.C. 1991. Line-source sprinkler irrigation technique for screening groundnut genotypes for drought tolerance. Paper presented at the national symposium on recent advances in drought research, 10–12 December, 1991, Kottayam, India.

Nageswara Rao, R.C., Williams, J.H. and Murari Singh 1989. Relationship between sensitivity to drought and yield potential in peanut genotypes under different drought patterns. Agronomy Journal, 81, 887–893.

Nageswara Rao, R.C., Williams, J.H., Wadia, K.D.R., Hubick, K.T. and Farquhar, G.D. 1993. Crop growth, water-use efficiency and carbon isotope discrimination in groundnut (*Arachis hypogaea* L.) genotypes under end-of season drought conditions. Annals of Applied Biology, 122, 357–367.

Nageswara Rao, R.C. and Wright, G.C. 1994. Stability of the relationship between specific leaf area and carbon isotope discrimination across environments in peanut. Crop Science, 33, in press.

Singh, M., Rao, R.C.N. and Williams, J.H. 1991. A statistical assessment of genotypic sensitivity of groundnut (*Arachis hypogaea* L) to drought in line-source sprinkler experiments. Euphytica, 57, 19–25.

Watterrott, J. 1991. Root respiration of groundnut as influenced by temperature, circadian rhythm, nitrogen source drought and genotype. Ph.D thesis submitted to University of Bonn, Germany.

Wright, G.C., Nageswara Rao, R.C., and Farquhar G.D. 1994. Water-use efficiency and carbon isotope discrimination in peanut under water deficit conditions. Crop Science. 33, in press.

Wright, G.C., Nageswara Rao, R.C. and So, H.B. 1993. Variation in root characteristics, and their association with water uptake and drought tolerance in four peanut cultivars. Paper presented at the 7th Australian Agronomy Conference, 19–24 September 1993, Adelaide, South Australia.

Drought Research on Groundnut at Tamil Nadu Agricultural University, and Drought Patterns in the Vriddhachalam Region

A. Arjunan*

In Tamil Nadu 1.03 million ha of groundnuts are grown, with an average pod yield of 1153 kg/ha. Mean yield per ha has been relatively static over the past few years: 1262 kg/ha in 1986 and 1160 kg/ha in 1991, for example. Considerable research effort has been invested to improve groundnut yields, but overall these efforts have not been successful. This is largely because this oilseed crop is predominately grown under rainfed conditions (650 000 ha) where monsoon rains received during the crop growth period are erratic and unevenly distributed, thus exposing crop to severe drought conditions (Figs 1 and 2).

In a study during the summer of 1985, when five groundnut varieties were grown under drought and watered conditions, it was found that crop growth rate was maximised during the period between 45 and 60 days after sowing, and subsequently declined until maturity (Srinivasan et al. 1987). When drought was imposed from 45–60 days after sowing, there was a decrease in leaf and stem dry weight, which was associated with lower pod weight. A high positive correlation was observed between crop growth rate and dry matter production, and pod yield at 30–45 days under irrigated and drought conditions (0.993* and 0.959**; 0.998** and 0.972**, respectively).

In experiments conducted during summer of 1985, when 11 groundnut genotypes were grown under drought conditions, it was found that the drought-tolerant varieties viz. VRI 2, JL 24 and Co 2 had higher root-to-shoot ratios than susceptible varieties (Arjunan et al. 1988). The more extensive and deeper root system observed in the tolerant varieties is considered to be an adaptive mechanism for the efficient absorption of water and nutrients under drought conditions. Indeed, leaf K^+ content and total cations were higher in the drought-tolerant genotypes, with the variety VRI 2 accumulating 1.71% of K^+ and 4.96% of total cations, compared only 1.21% and 3.67% for the drought-susceptible variety Co 1. The higher accumulation of leaf K^+ by tolerant genotypes may assist in the regulation of water loss through stomata. The results demonstrated the existence of a close association between leaf K^+ content and higher dry matter and pod yield under drought conditions (Arjunan et al. 1988).

In another study, conducted with 24 groundnut genotypes during the summer of 1986, ICG 4790 recorded the highest pod yield (8.54 g/plant) under drought conditions (Arjunan et al. 1987). This cultivar produced higher leaf area and dry matter, and these characters were positively correlated with pod yield (r = 0.38*). However, a negative correlation between transpiration rate and pod yield was also recorded (r = 0.30**). The tolerant cultivars ICG 4790 and ICG 1697 recorded the lowest transpiration rates of 5.76 and 5.74 µg/cm^2/s. By maturity, a greater number of functional leaves was observed in the cultivar ICG 4790, with this character being positively correlated with pod yield (r = 0.33**). This is not surprising, since photosynthates would have been available for podfilling at the last stage of crop growth.

To identify the physiological attributes associated with drought tolerance, studies were undertaken during the rainy season of 1990, when 25 cultivars from ICRISAT were grown under rainfed conditions. The crop experienced severe drought conditions, since there was no rain between 55 and 75 days after sowing. Highest pod yield was recorded in ICGV 86607 (5.46 g/plant), closely followed by ICGV 86635 (5.42 g/plant) and ICG 3556 (5.2 g/plant). These genotypes had higher leaf weight, dry matter, and relative water content, and had a larger number of functional leaves at harvest time (Arjunan et al. 1992). Further analysis has shown that dry matter was positively correlated with the pod yield under drought conditions. The high positive, yet indirect, effect of leaf weight on leaf area and hence transpiration rate, and of leaf area on dry matter, were also highlighted in this study.

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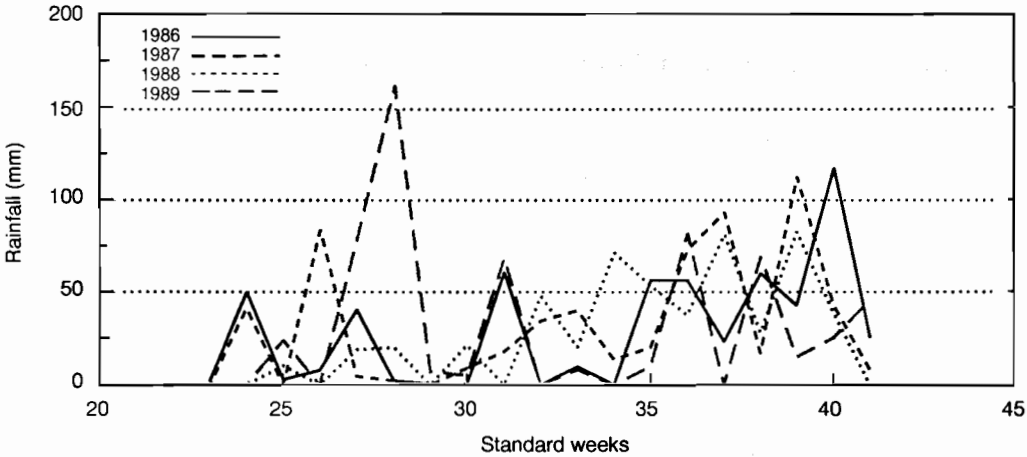

Figure 1. Rainfall distribution in Vriddhacham

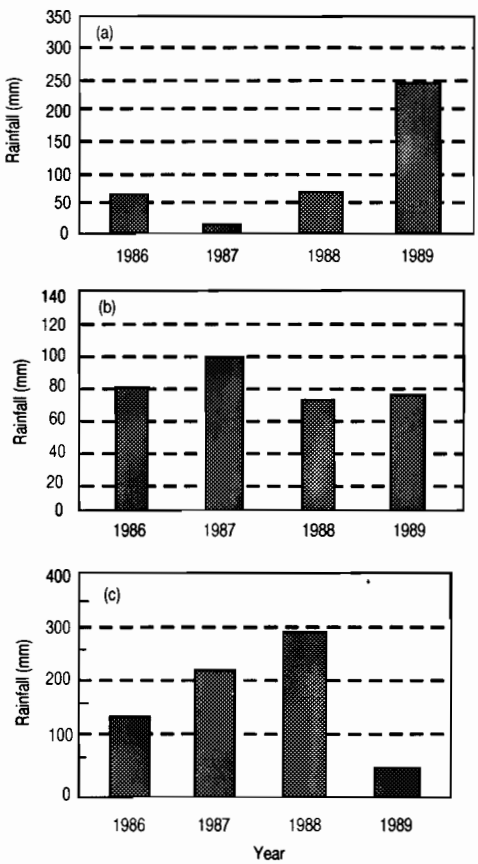

Figure 2. Rainfall distribution in Vriddhacham (a) during vegetative period, (b) during flowering period, and (c) during pod setting of groundnut

A seed-hardening technique has been developed at Tamil Nadu Agricultural University to over come early season drought in groundnut. The seed-hardening procedure involves soaking kernels in a 0.5% calcium chloride solution (half the volume of the seed) for 6 hours, keeping the kernels moist for 24 hours, and shade drying to original seed moisture content. The hardened seeds gave 95% field emergence, had higher seedling vigour, accumulated more total dry matter, possessed greener leaves for more efficient photosynthesis, and had deeper root systems for greater absorption of water and nutrients.

References

Arjunan, A., Manoharen, V. and Thengaveln, S. 1992. Field screening for drought resistance in groundnut. International Arachis Newsletter, 12, 11–12.

Arjunan, A., Srinivasan, P.S. and Vindiyavarman, P. 1988. Physiological aspects of drought tolerance in groundnut (*Arachis hypogaea* L.). Madras Agricultural Journal, 75, 5–8.

Arjunan, A., Vindiyavarmon, P., Selthupalthe Ronalijem, R. and Sivarem, M.R. 1987. Physiological indices for drought tolerance in groundnut (*Arachis hypogaea* L.). Paper presented at National Seminar on Physiology and Biochemistry of Oilseed Plants, held at Sinvekateswara University, Thirupathi, 5–7 February, 1987.

Drought Research on Groundnut at Andhra Pradesh Agricultural University, and Drought Patterns in the Tirupati Region

P.V. Reddy*

THE Regional Agricultural Research Station, Tirupati, is situated at 13°N latitude, 79°E longitude at an altitude of 182.9 m above mean sea level. It is the main research centre for the southern agroclimatic zone of Andhra Pradesh and lead centre for research for the state. In addition to developing improved varieties adapted to this region, the research mandate includes research on soil and moisture conservation practices and verification of these functions on other crops.

Groundnut is grown on about 450000 ha, mainly during the rainy season (July–November) in this zone. The average pod yield ranges from 600 to 1300 kg/ha in different parts of the zone. Though total crop failure is rare, dry spells of varying duration during the growing season are very common.

Details of the occurrence of dry spells at Tirupati centre during the last decade are presented in Table 1. The effect of drought on the growth and yield of groundnut crops depends on its intensity, duration and time of occurrence in relation to crop growth. Rainfall during the crop growth period (July–November) during the last decade has ranged between 338 and 694 mm. Interestingly, in drought years crop yield losses are always higher in farmers' fields than at the research station.

During the early part of the season, mean temperatures and evaporative demand are high (Table 2), then gradually decline throughout the reproductive phase of the crop. Average relative humidities range between 45 and 67% in the early phase of crop growth and increase to 55–80% during the later stages of crop growth.

Current Research Activities

Studies are in progress to evaluate the yield performance of all pre-release groundnut cultivars under mid-season and terminal water stress conditions. In these studies mid and end-of-season water stress is simulated by withholding irrigation. Screening of groundnut germplasm to identify suitable drought-tolerant parents for use in the breeding programs is also in progress.

Table 1. Dry spells exceeding 15 days, rainfall received and groundnut pod yields between 1981 and 1992 period at the Regional Agricultural Research Station, Tirupati.

Year	Dry spells exceeding 15 days					Rainfall	Pod yield
	July	Aug.	Sept.	Oct.	Nov.	(mm)	(kg/ha)
1981	N[a]	N	N	N	21	457	1291[b]
1982	16	38	22		18	674	1335[b]
1983	N	N	N	N	24	694	1291[b]
1984	N	22	20	25		648	1502[c]
1985	17	N	N	20	17	521	2101[c]
1986	25	25	N	20	20	454	1083[c]
1987	31	20	N	N	N	501	1834[c]
1988	N	N	N	26	19	427	2150[c]
1989	61		N	21	N	338	866[c]
1990	61		N	18	N	500	1537[c]
1991	N	26	22	N	14	479	1901[d]
1992	25	32	N	17	N	623	2141[d]

[a] N – Nil
[b] TMV2; [c] JL.24; [d] TPT.1

Research Highlights

Tirupati-1, a short duration, spanish bunch groundnut, was found to be tolerant to mid and end-of-season drought. In general, early types with small to medium sized pods (kernel weight 25–30 g/100 seed) were found to tolerate moisture stress better than genotypes with larger pods.

Drought periods can result in a prolonged crop duration. In the later part of the rainy season the biotic stresses, i.e. foliar diseases and insect pests, can severely limit pod yields. Thus, any new drought-tolerant cultivars need to have high levels of foliar-disease tolerance.

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Table 2. Ten-year (1981–90) average rainfall, temperature, evaporation and relative humidity during the rainy season at the Regional Agricultural Research Station, Tirupati

Month	Rainfall[a]	Temperature (°C)		Evaporation	Relative humidity	
	(mm)	Max.	Min.	(mm/day)	Forenoon	Afternoon
July	125.5 (8)	35.1	24.6	7.8	67	43
August	97.3 (6)	34.3	24.5	8.1	68	46
Sept.	171.3 (9)	33.9	23.5	6.3	76	53
Oct.	134.4 (7)	32.2	21.8	5.7	79	55
Nov.	175.7 (7)	29.8	19.2	4.8	80	57

[a] Figures in parentheses are number of rainy days.

Drought stress during the late pod-filling phase results in less reduction in pod yield compared with dry spells during the flowering and pegging periods.

At present there is a field recommendation to alleviate mid-season moisture stress by spraying 2% urea (1000 L/ha) 15 days after the onset of moisture stress, followed by another spray 10 days later. A 20% increase in pod yield has been reported in on-farm trials using this treatment.

Drought Research at National Research Centre for Groundnut, and Drought Patterns in Junagadh Region

Y.C. Joshi, P.C. Nautiyal and V. Ravindra*

THE National Research Centre for Groundnut (NRCG) is located at Junagadh, 21°31'N and 70°36'E. Drought is a major constraint for production of groundnut in this region. Drought can occur at any time during the growth period, with varying severity. Analysis of rainfall data for the past 26 years has shown that the average annual rainfall is about 850 mm, with July being the wettest month both in terms of total rainfall and number of rainy days. Total annual rainfall has ranged between 150 and 1550 mm. Rainfall probability studies have indicated a probability of 45, 41 and 14% occurrence of drought during the pod development, vegetative and pegging stages, respectively.

Groundnut is a highly drought-tolerant legume. The water requirement of this crop has been reported by various workers to be in the range 256–450 mm. It has been found that groundnut responds quickly to drought by increasing leaf diffusive resistance, reducing transpiration and folding leaflets. Leaf orientation parallel to the sun beam greatly reduces the radiation load, as well as transpiration rates and leaf temperatures. The plant therefore possesses numerous drought adaptive mechanisms that allow it to survive water stress conditions. However, the major requirement of agriculture is for crops to produce high pod yields under stress conditions, and survival mechanisms alone may not necessarily achieve this objective.

NRCG has a major research program addressing the problem of drought in groundnut. Its objectives are:

- screening of germplasm lines, including initial and advanced screening; and
- identification of parameters for, and mechanisms of, drought tolerance, including studies on aspects such as pod yield, dry matter production, flowering, water relations, leaf area, leaf wax, leaf folding, proline accumulation, thermostability, leaf cell sap pH, leaf air-temperature difference, and photosynthesis.

Some highlights of these studies follow.

Screening for Drought Tolerance

Screening of germplasm lines under rainfed and simulated drought conditions is a continuing activity. This is done in two steps.

- Initial screening: 100–150 lines are screened at one time. The screening is done under both rainfed and simulated drought conditions. The lines with superior pod yield are promoted to the advanced screening stage.
- Advanced screening: selected germplasm lines obtained from the initial screening are studied in detail.

Mechanisms of Drought Tolerance

Studies on comparative changes in some physiological characters under water stress have been conducted in a drought-tolerant and a sensitive genotype.

It was found that the resistant genotype maintained higher leaf relative water contents (RWC) at lower leaf water potentials. The leaf-to-air temperature difference in the tolerant genotype was found to be 1–2°C, whereas in the sensitive genotype there was a progressive increase from 1 to 4°C as soil-water deficits increased. This shows that the tolerant genotype was able to maintain lower leaf-to-air temperature differences. RWC of the tolerant genotype was maintained around 80%, despite severe stress conditions. In the sensitive genotype, RWC declined to around 70%. The tolerant genotype was also able to maintain higher photosynthetic activity under stress conditions. It was interesting to note that although leaf conductance differences in these genotypes were not large, there were significant differences in the rate of photosynthesis. The recovery after relief of water stress

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was faster in the tolerant genotypes. The physiological mechanisms of maintenance of high RWC at low leaf-water potential, and higher photosynthetic activity, confer an ability to withstand water deficits on the resistant genotype.

Genetic Variations

Germination

Genotypic differences in the germination, root length and seedling vigour index (SVI) were observed under water-deficit conditions. In our study, SVI in the genotypes ranged from 21 to 262, which suggests that there may be scope to select genotypes for rainfed situations when drought is encountered immediately after sowing.

Photosynthesis

The photosynthetic rate (P_n) of 30 spanish cultivars was recorded in the kharif and summer seasons under well-watered conditions. Large genotypic differences in P_n were observed, with P_n being higher in summer compared with kharif seasons. For example, P_n ranged from 9.52–26.30 in Kharif and 20.69–34.31 CO_2 mg/m^2/hour during summer.

Specific leaf area (SLA)

Genotypic differences for SLA have been observed. These differences were more pronounced during the pod-filling phase.

Thermostability

Studies on relative injury (RI) in groundnut leaves have shown that RI is greater during earlier than later growth stages. This response indicates that there may be a degree of acclimatisation as ontogeny proceeds. The magnitude of genetic differences in RI was greater at later stages of growth.

Leaf drying — an adaptive process or an indicator of water stress tolerance?

In a recent study, variability in the extent of leaf drying was observed. Interestingly, the germplasm lines whose leaves dried rapidly yielded more than in genotypes whose leaves remained green. This finding may indicate the existence of an adaptive mechanism that mobilises carbon from the foliage to the developing pods.

The above-mentioned studies revealed the degree of genetic variability for some of the physiological characters which may be useful for higher yields under water-deficit conditions. There is great scope to utilise this variability for crop improvement.

Imposition of Water Stress for Enhancement in Yield

In groundnut, it is often observed that whenever rain occurs following a period of drought, profuse flowering takes place. We have attempted to make use of this observation by imposing short-term water stress during the vegetative stage, such that flowering becomes synchronised. Experimental results have shown this treatment can bring substantially higher pod yields. Genotypic differences in this response have also been observed. As well as higher pod yields this management practice has resulted in significant water savings.

Our findings to date indicate that the following features of groundnut plants may confer adaptation to drought stress:

- ability of the leaves to maintain turgor at low leaf water potentials and soil water status
- minimum leaf-to-air temperature differentials
- maintenance of photosynthetic capacity
- strong reproductive sink and better partitioning
- means of reducing radiation load.

Drought Research at Maharashtra Agricultural University, and Drought Patterns in the Jalgaon Region

Y.M. Shinde and S.S. Patil*

Drought is one of the most important factors limiting crop production in rainfed regions. Water may become a limiting factor for plants in arid and semi-arid regions. Water plays a vital role as a solvent in which mineral nutrients, salts, and other foodstuffs are translocated in solution into the plant. Its physiological significance in plant life means water deficiencies will have marked effects on plant growth.

In Maharashtra there are two major climatic zones where groundnuts are cultivated: an area receiving rains from the southwest monsoon (Jalgaon, Nasik, Nagpur, Pune, Vidarbha and part of Marathwada), where non-dormant bunch varieties of 90–100 day maturity are grown; and an area receiving rains from both the southwest and northeast monsoons (Sangli, Satara, Kolhapur, Solapur and part of Marathwada region), where dormant, semi-spreading varieties of 125–140 day maturity are grown.

Jalgaon centre is located in an assured rainfall zone, and conducts research on groundnut and sesamum in the kharif. The Jalgaon district has a hot, dry climate. Maximum temperatures (May) vary between 40.6 and 46.1°C, while minima of 4–6.7°C occur in December. The rainy season is from mid-June to mid-October. Mean annual rainfall is 815 mm (Table 1).

The following section gives an account of the type of seasonal variability occuring over the past 10 years in the Jalgaon region, and its impact on groundnut crops.

1980–82 : Season diverged widely from normal. A prolonged dry spell from 11 September onwards affected peg penetration, pod formation and development of crop.

1981–82 : Evenly distributed rainfall during the crop growth period. In general, season was quite favourable for crops such as groundnut and sesame.

1982–83 : From 25 June there was no rain for 15 days. Late sowing of remaining trials undertaken after rain on 10 July. Dry spells after 23 August and 23 September resulted in hardening of the soil.

1983–84 : Dry spell in last week of June. June rainfall was well below average (61.8 mm as against 151.1 mm for the long-term average).

1984–85 : Season diverged widely from normal. There were prolonged dry spells with only brief intermittent showers. After sowing there was a dry spell of about 13 days up to 2 August. The unfavourable season affected pod development.

1985–86 : Prolonged dry spells from 28 June–17 July, and from 9 August–4 October, adversely affected crop growth and resulted in low yields. Rainfall was 459.4 mm in 29 days, compared with long-term average of 815 mm.

1986–87 : There was a prolonged dry spell from 19 August until harvest, with only limited intermittent showers between 17 June–30 September. Drought periods had a pronounced adverse effect on crop growth, pegging and, to some extent, pod development.

1987–88 : Groundnuts were sown from 18–22 June. There was uneven distribution of rain and dry periods during flowering and pegging. Because of intermittent dry periods at critical stages, pod yields were only fair.

1988–89 : Total rainfall received during the year was much higher than average rainfall (723 mm). No dry periods were recorded during kharif.

1989–90 : Sowing was completed in the 1st week of July. Lack of rain in October hindered pod development. A total of 667.1 mm was received from June to October in 64 days.

1990–91 : Rainfall was higher than normal. The monsoon had commenced by 1 June 1990 and 133.2 mm of rain were recorded during 22, 23 and 24 meteorological weeks. There were no rains in the 25th week.

1991–92 : After 26 August rainfall ceased, resulting in severe drought periods. The early end of the monsoon had a severe effect on yield.

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Table 1. Rainfall pattern at Jalgaon

Year	Month										Total	
	June		July		August		September		October			
	R.F.[a]	R.D.[b]	R.F.	R.D.	R.F.	R.D.	R.F.	R.D.	R.F.	R.D.	R.F.	R.D.
1980	196.2	16	89.6	14	252.0	21	69.4	4	–	–	657.0	59
1981	62.2	6	231.2	24	364.4	21	75.0	12	24.0	6	807.6	75
1982	250.0	6	168.6	16	133.3	15	32.4	2	26.5	5	650.5	54
1983	61.8	7	276.4	24	267.6	20	202.2	15	50.4	7	860.2	75
1984	66.4	6	203.2	12	172.4	21	25.2	10	47.0	5	527.4	60
1985	101.4	5	163.6	16	84.1	15	6.9	5	70.4	5	450.4	49
1986	106.4	12	196.6	12	164.1	8	47.0	3	–	–	611.7	42
1987	158.0	6	73.4	7	290.2	12	6.6	2	96.0	5	733.4	42
1988	136.7	8	374.5	21	82.6	10	298.4	14	45.0	3	944.0	59
1989	153.4	7	155.8	12	268.1	17	89.0	6	0.8	–	729.7	46
1990	168.5	7	176.4	9	447.1	19	82.5	6	140.1	7	1080.6	54
1991	203.1	9	402.8	15	103.9	14	15.8	2	–	–	731.4	40
1992	230.0	6	133.8	11	147.4	12	195.8	5	70.8	3	814.8	38

[a] Rainfall (mm)
[b] Rainy days (no.)

In Maharashtra, groundnut was cultivated over an area of 636000 ha during the kharif season, with a total production of 413 kt, and an average yield of 648 kg/ha during 1991–92. The area, production and productivity during the last 10 years are given in Table 2.

Table 2. Area, production and productivity of kharif groundnut during the 1980–1992 period in Maharashtra State

Year	Area ('000 ha)	Production ('000 t)	Productivity (kg/ha)
1980–81	6.65	4.06	610
1981–82	6.76	4.35	643
1982–83	6.17	4.19	680
1983–84	6.13	5.26	859
1984–85	6.27	5.73	914
1985–86	6.26	4.22	673
1986–87	6.12	3.77	616
1987–88	5.94	5.28	888
1988–89	6.61	5.99	907
1989–90	6.39	6.18	968
1990–91	6.29	5.82	926
1991–92	6.36	4.13	648

Objectives of the AICORPO Project Jalgaon

The objectives of this project are to develop:

- high-yielding varieties possessing desirable characteristics such as high shelling percentage, high oil content, early maturity, and tolerance to aphids and diseases such as leaf spot, rust, *Aspergillus* and *Sclerotium* wilt; and
- suitable agronomical practices and plant protection measures under the changing climatic/seasonal conditions.

From 1972 onwards, there has been an early end to the monsoon (from August) with dry periods ranging from 6 to 30 days. The erratic nature of the monsoon, along with its early end, has resulted in a changing of the research effort to identify early maturing, synchronised basal flowering genotypes. As a result of continuing efforts, scientists at the Jalgaon Research Centre have identified the groundnut cultivar JL-24, which is capable of avoiding droughts arising from an early cessation of the monsoon. Some of the yield data from varietal experiments comparing JL-24 with SB-XI are given in Table 3.

The Maharashtra region needs two types of groundnut varieties.

- For an area receiving predominantly the south-west monsoon, varieties are needed with the

Table 3. Comparative yield data (kg/ha) for cultivars JL-24 and SB-XI

Variety	1975		1976		1977		1978	
	No. of trials	Yield	No. of trials	Yield	No. of trials	Yield	No. of trials	Yield
JL-24	1	2356	2	1892	7	1893	13	1201
SB-XI		1256		505		913		647

following attributes: early maturing, high yielding, limited dormancy, drought tolerant, pest and diseases resistant, spanish bunch.

- For areas receiving both the southwest and northeast monsoons, attributes are: early maturing, high yielding, limited dormancy, drought resistance/tolerant, virginia bunch and/or runner tolerance to diseases and pests.

Drought Research at Rajasthan Agricultural University, and Drought Patterns in the Jaipur Region

S.N Sharma and K.N. Sharma*

RAJASTHAN is an important groundnut-producing state in India, with approximately 253000 ha under groundnut cultivation. About 90% of the area is grown under rainfed conditions, with average pod yields ranging from 774 to 942 kg/ha over the past five years. Although the crop is well adapted to arid conditions, it responds well to irrigation. The maximum yield potential in the Shri Ganganagar, Hanumangarh and Suratgarh areas ranges between 1600 and 1900 kg/ha.

The close association between rainfall pattern and yield of groundnut indicates that water is the major constraint to production. The average rainfall at Durgapura during the last five years has ranged between 418 and 807 mm, and 95% of the precipitation was received during July–September. Consequently, terminal water stress, which limits groundnut productivity, occurs commonly in Rajasthan state.

Though drought severely reduces groundnut yield, little progress has been made in breeding drought-adapted cultivars at Durgapura.

Drought Research

It is well established that photosynthesis declines during pod development in grain legumes, and is probably associated with strong sink demand by developing pods. However, little is known on the extent to which environmental conditions impose a ceiling on the functional activity of plants or the changes that occur in the photosynthetic characteristics. In particular, adaptation of legume crops to high temperatures and water-limiting conditions in the arid and semi-arid tropics is not well understood.

We have therefore tried to analyse the limitations to photosynthesis in the field and considered the adaptive significance of these limitations. For example, a chickpea crop was raised in the field following recommended agronomic practices, and observations were made on single leaves from 60 days after sowing (DAS) (flowering) to 128 DAS (maturity) using an infra-red gas analyser.

Reduced photosynthetic rates during pod development, and an accelerated senescence, were induced by plant water deficits and high leaf temperatures. A positive correlation between intrinsic water-use efficiency (WUE) and interception of photosynthetically active radiation, and relative water content, was obtained in this study (Sharma and Singh 1989).

The difference between leaf and air temperatures was reduced from about 2°C to 1°C at 114 DAS which was probably another reason why photosynthetic rates declined at a faster rate after 114 DAS. The relationship between leaf conductance (g_s) and photosynthetic rate (A) was found to be curvilinear during this period, indicating a capacity for adaptation to water and high-temperature stress.

In conclusion, it appears that both water and high-temperature stress can cause a rapid decline in photosynthetic rates under field conditions. It may therefore be appropriate to screen germplasm for their adaptability under such stress conditions in the field.

References

Sharma, S.H. and Singh, G. 1989. Limitations of gas exchange in intact leaves during ontogeny of field-grown chickpeas. Journal of Experimental Botany, 40(221), 1399–1406.

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Carbon Isotope Discrimination as an Indicator of Water-use Efficiency

^{13}C Isotope Discrimination in Plants — a Potential Technique to Determine Water-Use Efficiency

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ATMOSPHERIC CO_2 contains approximately 1.1% of non-radioactive isotope ^{13}C and 98.9 per cent of ^{12}C. During photosynthesis, plant discriminate against ^{13}C because of small differences in chemical and physical properties imparted by the difference in mass. This discrimination can be used to assign plants to various photosynthetic groups.

Recent analysis of ^{13}C discrimination (Δ) during photosynthesis indicated that it could be a reflection of CO_2 diffusive processes and H_2O and carboxylation reactions, and hence could be used to assess differences in water-use efficiency (WUE).

Isotope Composition

The ^{13}C content is usually determined with a mass spectrometer specially designed for high precision measurements of the ratio, R, defined as:

$$R = {}^{13}CO_2/{}^{12}CO_2$$

The plant materials have to be converted to CO_2 by combustion for assessing the isotope composition. In general, R is low in organic sources. The atmosphere displays a lower R than the often-used standard PDB (Pee Dee beleminite, a fossil limestone from South Carolina). The R in this standard is 0.01124 and in many of the natural plant material it is approximately 0.0112, suggesting only very minor changes in the R value. Because the differences in R are very small, the $^{13}C/^{12}C$ ratios in a sample are compared with $^{13}C/^{12}C$ ratios of standard and expressed as ^{13}C in units per mil (‰):

$$^{13}C = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000$$

Units. Organic matter is invariably depleted in ^{13}C compared with PDB, thus ^{13}C values of organic material are negative. More negative ^{13}C = less ^{13}C in the sample compared with standard and hence more discrimination. Less negative ^{13}C = more ^{13}C in the sample and hence less discrimination.

Range of ^{13}C values in atmosphere and plants:

- atmospheric CO_2 has a ^{13}C value between – 6.4 and – 7.0‰
- in C_3 plants = – 22 to – 44‰ (mean –28‰)
- in C_4 plants = – 9 to – 19‰ (mean –14‰)
- CAM plants = mean of approx. –11‰.

^{13}C discrimination — Δ. While ^{13}C value is an expression of isotope composition, relative to standard isotope fractionation, discrimination (Δ) is the difference in ^{13}C value between the source and product of a particular reaction or process.

$$\Delta = \frac{{}^{13}C_{source} - {}^{13}C_{product}}{1 + {}^{13}C_{product}}$$

$$= \frac{-0.0080 - (-0.0300)}{1 - 0.0300}$$

$$\Delta \times 10^3 = 22.68$$

If the ^{13}C value of source (air) = 7‰, and ^{13}C of product (plant) = 27‰, then the fractionation (Δ) is 20‰.

Carbon Isotope Discrimination (Δ) during Photosynthesis

The principal components affecting the overall isotope discrimination during photosynthesis are diffusion of CO_2, interconversion of CO_2 to HCO_3 (solubility) and fixation of CO_2 by phosphoenolpyruvate (PEP) carboxylase or RuBisCo. The assimilation product contains less ^{13}C compared with the source i.e. CO_2 in the air.

Plants with C_3, C_4 and CAM photosynthetic

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pathways show characteristically different discriminations against ^{13}C during photosynthesis. Apart from the differences in diffusivity, the major factor contributing to these differences in discrimination between C_3 and C_4 plants is carboxylation site. Since the discrimination of PEP carboxylase is relatively lower than RuBISCO, discrimination is always lower in C_4 than in C_3 plants. Since CAM plants are facultative C_4 plants, the discrimination values under stress (dark CO_2 fixation through PEP carboxylase) are always low, and under well-watered conditions (light CO_2 fixation by RuBISCO) are close to C_3 plants.

Relationship between Δ and WUE

WUE is the ratio of total dry matter (DM) produced to water transpired. Two physiological processes — the assimilation rate (A) and transpiration rate (E) —are associated with WUE. At leaf level, WUE can be expressed as:

$$WUE = (P_a - P_i)/1.6V$$

where P_a and P_i are the partial pressures of CO_2 in the ambient air and intercellular spaces, respectively, and V is the vapour-pressure deficit.

Relationship between Δ and P_i/P_a

The ratio of P_i/P_a is predominantly determined by the conductance, g_s, and intrinsic carboxylation efficiency of the leaf. Differences in g_s which affect the rate of diffusivity and the availability of substrate can influence the extent of discrimination.

$$\Delta = (a - d) - (b - a)P_i/P_a$$

where a, b, and d are constants for the discrimination against $^{13}CO_2$ during diffusion of CO_2 into the leaf, carboxylation, and diffusion of dissolved CO_2, respectively, and P_i and P_a are the intercellular and ambient CO_2 partial pressures.

WUE is predominantly controlled by P_i/P_a, which in turn determines the Δ. There is therefore a strong correlation between Δ and WUE.

$$WUE = [(1 - \theta)(P_a - P_i)]/1.6V$$

θ = is the proportion of fixed CO_2 lost in respiration

V = vapour pressure deficit

$\Delta = (a - d) - (b - a)P_i/P_a$

therefore

$$WUE = [(1 - \theta)(b - d - \Delta)]/1.6V(b - a)$$

It has been demonstrated that WUEs measured at leaf level (Johnson et al. 1990) or in containers and/or studies in the field (Condon et al. 1990) were inversely related to Δ, suggesting potential of a technique for determining variation in WUE of C_3 plants. A high negative correlation between WUE and Δ has been reported in several species and further evidence suggests that Δ is under genetic control (Hubick et al. 1988).

In view of its relation with P_i/P, intrinsic differences in conductance (g_s) also could be determined by gas exchange methods with a certain degree of accuracy, as Δ and g_s are positively related (Read et al. 1991).

Because of diurnal and seasonal variations in assimilation and g_s, and therefore in P_i/P_a, these parameters may not give an integrated WUE over a period of time. In this context, the Δ has potential as a tool for determining the variations in gas exchange characteristics and WUE in C_3 plants.

Measurement of Water-use Efficiency in Crops

The efficiency with which crops use water (WUE) is expressed as the ratio of biomass produced (g) to the amount of water transpired (kg). In the literature, several related terms are used to refer to WUE depending on the type of experimental material — at single leaf, isolated plant, or canopy level.

At a given level of transpiration (T), differences in WUE can contribute to large differences in crop growth rates of genotypes and species [following the equation, pod yield = $T \times$ WUE $\times$ harvest index (HI)]. Therefore, identifying genotypic variation in WUE assumes considerable importance, especially in situations, where water is limiting.

Several terms are used in this context viz., transpiration ratio, transpiration efficiency and water-use efficiency.

$$\text{WUE} = \frac{\text{Dry matter produced (g)}}{\text{Water lost in transpiration (kg)}}$$

$$\text{Transpiration ratio (RT) or transpiration quotient (TQ)} = \frac{\text{Water used in transpiration (mL)}}{\text{Dry matter produced (g)}}$$

$$\text{Transpiration efficiency (TE)} = \frac{\text{mMoles of carbon assimilated}}{\text{Moles of } H_2O \text{ transpired}}$$

WUE has often been examined from various

points of view and there is considerable variation and ambiguity in the units used. The term water-use efficiency is used in different contexts by hydrologists, agronomists and physiologists.

In a hydrological context WUE has been defined as the ratio of the volume of water used productively (i.e. transpired and evaporated, from the area under study) to the volume of water potentially available for that purpose, that is, that reaching the crop growing region via rainfall and irrigation plus that available from the soil (Stanhill 1986).

In an agronomic context WUE of crops is addressed solely on the basis of the economic yield per unit of water applied or rainfall received in the growing season (French and Schultz 1984).

Use of evapotranspiration in the above context often results in considerable variability in WUE, because evaporation is affected by leaf cover and frequency of soil wetting, independently of transpiration (Turner 1986).

In a crop physiological context WUE can be defined at the level of a single leaf or at the whole plant or crop level. At the leaf level it is the ratio of carbon assimilated to water lost in transpiration, and is expressed as mg CO_2/g H_2O, or mmol CO_2/mol H_2O.

At the canopy level, WUE is the ratio of the total dry matter (including roots) per unit of water transpired. However, because of the difficulty in accurately measuring the root biomass in the field, WUE is usually calculated on the basis of dry matter excluding roots. Variation in root:shoot ratio among genotypes can result in erroneous estimation of WUE. A second complication arises from the difficulty in delineating evaporation from total evapotranspiration (Turner 1986).

At the single leaf level, WUE can be considered as micromoles of carbon assimilated per mole of H_2O transpired or mg of CO_2 fixed per g of H_2O.

A few important principles need to be considered for the study of WUE at the gas exchange level. Gastra (1959) studied the diffusion of CO_2 and H_2O through the stomata and the physical laws influencing transfer rates. The diffusivity of water vapour is 1.56 times that of CO_2 or conversely the diffusivity of CO_2 is 0.64 times that of water vapour.

Determination of WUE Using Gas Exchange Techniques

Photosynthetic rate and stomatal conductances can be measured using a portable carbon dioxide analyser (models ADC LCA-2 or LICOR-6200). These instruments can instantaneously measure CO_2 and water vapour exchange. In both instruments a known leaf area of a single intact leaf is inserted into a chamber housing the sensors needed to measure photosynthetically active radiation, relative humidity and temperature. However, since the gas exchange parameters are dynamic, spot measurements of A/E values may not accurately represent long-term WUE.

Gravimetric Method for Determining the Intrinsic WUE in Containers or Pot Studies

A gravimetric method is often adopted to measure WUE at a whole-plant level in plants grown in containers. WUE is assessed as the change in biomass relative to the amount of water transpired during the same period.

Initial and final dry matter are obtained by destructive plant sampling. Transpiration from the pots is determined by weighing pots at frequent intervals and adjusting the water loss for soil evaporation from pots without plants grown in them.

In pot experiments the canopy microclimate may not exactly represent that of a field situation because of reduced competition for roots in pots, limited growth of roots in pots etc. Nevertheless, container studies have some advantages. For example, genotypic differences in WUE can be accurately assessed since soil evaporation losses and root biomass can be effectively measured.

References and Further Reading

Condon, A.G., Farquhar, G.D. and Richards, R.A. 1990. Genotypic variation in carbon isotope discrimination and transpiration efficiency in wheat. Leaf gas exchange and whole plant studies. Australian Journal of Plant Physiology, 17, 9–22

Farquhar, G.D., Ehleringer, J.R. and Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology, 40, 503–537.

French, R.J. and Schultz, J.L. 1984. Water use efficiency of wheat in mediterranean type environment. I. The relationship between yield, water use and climate. Australian Journal of Agricultural Research, 35, 743–764.

Gastra, P. 1959. Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature and stomatal diffusive resistances. Meded Landbouhogesd. Wagenengen, 59,1–68.

Hubick, K.T., Shorter, R. and Farquhar, G.D. 1988.

Heritability and genotype × environment interactions of carbon isotope discrimination and transpiration efficiency in peanut (*Arachis hypogea* L). Australian Journal of Plant Physiology, 15, 799–813.

Johnson, D.A., Asay, K.H., Tieszen, L.L., Ehleringer, J.R. and Jefferson, P.G. 1990. Carbon isotope discrimination: potential in screening cool season grasses for water-limited environments. Crop Science, 30, 338–343.

Meinzer, F.C., Goldstein, G., Grantz,D.A. 1990. Carbon Isotope discrimination in coffee genotypes grown under limited water supply. Plant Physiology, 92: 130–135.

O'Leary, M.H. 1981. Carbon isotope fractionation in plants. Phytochemistry, 20, 553–567.

O'Leary, M.H. 1988. Carbon isotopes in photosynthesis. Bioscience, 38, 328–336.

Read, J.J., Johnson, D.A., Asay, K.H. and Tieszen, L.L. 1991. Carbon isotope discrimination, gas exchange and water use efficiency in crested wheat grass clones. Crop Science, 31, 1203–1208.

Stanhill, G. 1986. Water use efficiency. Advances in Agronomy, 39, 53–83.

Turner, N.C. 1986. Crop water deficits: a decade of progress. Advances in Agronomy, 39, 1–43.

Water-use Efficiency — Its Importance in Drought Resistance in Groundnut and Other Food Legumes

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THE traditional solution to water shortages has been irrigation. However, its use in many cropping areas is limited because it is either not available, or the large capital costs of equipment and pumping preclude its widespread use. There is therefore an increasing interest currently being directed toward the breeding of plants that are capable of yielding well under water-limited conditions. Improvement in water-use efficiency (WUE), as discussed in the previous paper, is one such attribute that could potentially lead to improved yield under water-limited conditions.

WUE is defined here as the ratio of total dry matter to the total amount of water transpired. In the following paper we restrict our discussion to that of the above definition, which is often more correctly referred to as transpiration efficiency. WUE has also been referred to as evapotranspiration (ET) efficiency (Tanner and Sinclair 1983) which includes water loss by soil evaporation (E_s). In this context, we should be aware that crop WUE can be significantly increased by reducing the proportion of soil evaporative losses (e.g. by surface mulches or planting in the cooler part of the season) without altering the innate transpiration efficiency of a crop or cultivar. Richards (1991) provides an excellent review of this topic elsewhere.

Factors Affecting WUE

To examine the factors contributing to variation in WUE, the following expression adapted from Hubick et al. (1986) can be used:

$$WUE = A/g = [p_a(1 - p_i/p_a)]/[1.6(e_i - e_a)]$$

This is the WUE of a whole plant where e_i and e_a, p_i and p_a are the intercellular and atmospheric vapour pressures for water and CO_2, respectively. This equation indicates that WUE can be increased by reducing either (a) $e_i - e_a$ and/or (b) p_i/p_a.

Decreasing $e_i - e_a$

Richards (1991) suggested there are two ways to improve WUE that rely on minimising the vapour pressure difference between leaf and air. The first relies on utilising the seasonal variation in $e_i - e_a$. Thus, the greater the crop growth when $e_i - e_a$ is low, then the higher is the crop WUE. The simplest way to achieve this is to plant crops early in the season, if possible, when $e_i - e_a$ is substantially lower than later in the season. The work of Keatinge and Cooper (1983) illustrates this effect in chickpea. The second way that $e_i - e_a$ can improve WUE is by reducing the radiation load on leaves and thereby reducing tissue temperature. The breeding of increased waxy covering on the cuticle (Johnson et al. 1983) and pubescence (Ghorashy et al. 1971) provide good examples. Similarly, active leaf movements which reduce radiation load and reduced stomatal sensitivity to drought may also reduce $e_i - e_a$.

Decreasing p_i/p_a

The atmospheric vapour pressure of CO_2 (p_a) is very stable over the season, while p_i changes substantially, and is largely determined by the relationship between the stomatal conductance (g_s) and the assimilation rate (A) of the leaf. WUE therefore depends upon the balance between A and g_s, which in turn determines the magnitude of p_i. Increases in A relative to g_s cause p_i to fall and WUE to increase. Similarly, a decreased g_s for a small change in A will also reduce p_i and increase WUE (Farquhar et al. 1989).

Genotypic Variation in WUE

Variation in WUE among genotypes of the same species was first documented in the pioneering

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work of Briggs and Shantz (1913), although the question of whether it could be used as a selection trait in the breeding of drought-tolerant genotypes has been argued about since (DeWit 1958; Fischer and Turner 1978; Tanner and Sinclair 1983). Recent evidence, however, has reconfirmed Briggs and Shantz's work, and unequivocally demonstrated substantial genotypic variation in WUE exists among many C_3 species [e.g. wheat, barley, rice, sunflower, cotton, tomato, beans, groundnut; see Hall et al. (1993) for a review of this subject].

The accurate measurement of WUE in pots is time-consuming, and values vary with environmental conditions. Measurement of WUE in the field is even more difficult, and additionally, current techniques available to estimate T and E_s are not very precise. Thus, to effectively exploit variation in WUE in large-scale breeding programs, breeders require an easily measured correlated trait. Such a correlated trait has recently been discovered, when Farquhar et al. (1982) showed that isotopic discrimination against ^{13}C (Δ) during photosynthesis was closely correlated with WUE. The Δ measurement provides an integrated measure of p_i, and hence WUE, over the life of the plant. This research has therefore raised the possibility of using Δ as a rapid and non-destructive trait for selection of WUE in large-scale breeding programs. Much of this pioneering research has been conducted in groundnut within ACIAR-funded projects. A summary of the findings of this research follows.

Groundnut (*Arachis hypogaea* L.)

Detailed experiments during the ACIAR funded projects on legume water-use efficiency (Project No. 8550) and groundnut improvement in Indonesia (Project No. 8834) provided unequivocal evidence that substantial variation in WUE exists, and that WUE and Δ are well correlated in diverse peanut cultivars grown under well-watered and droughted conditions in the glasshouse (Hubick et al. 1986, 1988) and the field (Wright et al. 1988, 1991, 1994). For instance, cultivar variation in WUE ranging from 1.9 to 3.7 g/kg has been measured in diverse peanut germplasm under field conditions. Genetic studies have also shown Δ is highly heritable ($h^2 = 0.81$) and has small genotype by environment interaction, indicating its potential for selection is good (Hubick et al. 1988).

It was also shown that specific leaf area (SLA, cm^2/g) or 'leaf thickness' was extremely well correlated with WUE and Δ over a wide range of cultivars and environments (Wright et al. 1988; Wright, Hubick et al. 1992; Nageswara Rao and Wright 1994). This observation highlights the possibility of using SLA as an even more rapid and inexpensive technique for selection of WUE. This finding has significant implications for peanut breeding programs in developing countries where access to, and resources to purchase and maintain, mass spectrometers are limited (Wright, Sarwanto et al. 1992; Wright, Hubick et al. 1992).

Being able to measure WUE on a wider range of groundnut cultivars has made it possible to detect an apparent negative association between WUE and HI. Although the range of germplasm tested was relatively small, a consistent trend was observed in a number of glasshouse and field studies. A preliminary crossing program showed that the negative association was consistent through to the F_4 generation, and no evidence that the linkage could be broken by breeding was found (Wright, Hubick et al. 1992). The moderate strength of the negative correlation between WUE and HI in this study ($r = -0.55$) and a similar genetic study conducted earlier in the project (Hubick et al. 1988), suggests that concurrent improvement in these traits may be difficult but should be possible. Indeed, the association should be able to be broken since cultivars such as UF78114-3 and VB-81 have moderately large WUE and HI. Further research to understand the nature of this correlation is needed before selection based solely on WUE can be recommended. On the basis of our preliminary findings, selection for low Δ or low SLA may improve total biomass, while having minor impact on pod yield. Such information may, however, be appropriate in some developing countries where both pod yield for human consumption and vegetative yield for animal fodder need to be maximised.

Other food legumes

The ACIAR-funded project on legume WUE (PN8550) studied the extent of cultivar variation in Δ in a number of legumes including *Vigna* species, cowpea, mungbean, and pigeonpea (Farquhar and Hubick 1988). These surveys revealed there was substantial genetic variation ranging from 25 to 50%, depending on the species. Detailed studies to determine whether the observed variation in Δ was correlated with whole plant WUE were not, however, conducted during this project.

Since the conclusion of ACIAR Project No. 8550 in 1988, there has been active worldwide

research aimed at studying cultivar variation in WUE, and its correlation with Δ in a number of important food legume crops. There are many aspects of this research requiring clarification. A brief review follows of the current literature on this topic for the legume crops we plan to study in the new project.

Cowpea (Vigna unguiculata *L.*). Large genotypic differences in Δ have been measured under irrigated and droughted conditions in the field at Riverside, California, USA (Hall et al. 1990). Based on theoretical analyses, the differences in Δ could reflect potential differences of 67% in WUE. Genotype rankings for Δ were similar under wet and dry conditions, indicating genotype x environment interaction was low. High broad sense heritabilities ($h^2 = 0.76$) were also measured under wet and dry conditions.

Studies with a cowpea mutant and parent demonstrated the expected association between CO_2 assimilation rate (A)/conductance to water vapour (g) and Δ for drought induced effects but not for genotypic effects (Kirchhoff et al. 1989). Hall et al. (1992) also observed a significant drought-induced increase in A/g among a wider range of cowpea genotypes, which was due to substantial decrease in stomatal conductance to water vapour. Despite measuring relatively large differences in Δ among genotypes, there were only small and inconsistent genotypic differences in A/g. Subsequent pot studies, however, have found that significant genotypic variation in whole plant WUE exists, and is strongly correlated with Δ ($r = -0.93$) in a manner expected on the basis of theory (Ismail and Hall 1992). Although highly significant genotypic differences in SLA were observed in the pot study, they were not associated with differences in WUE (or Δ). It is thought variation in WUE in cowpea occurs due to both variation in stomatal conductance to water vapour and photosynthetic capacity (Ismail and Hall 1992).

The current thinking is that Δ offers a convenient method to screen for WUE in cowpea breeding programs. There have, however, been no studies to verify whether genotypic differences in WUE and Δ measured in pots are occurring in the field canopy situation. Such studies are urgently required before Δ can be confidently recommended as a selection trait in future breeding programs. Also, the extent of any negative associations between WUE and other components in the physiological model needs to be addressed.

Navybeans (Phaseolus vulgaris *L.*). Navybean is not a drought-tolerant species, but is nonetheless grown over a wide range of habitats where the crop is exposed to seasonal droughts (Markhart 1985). Frequent drought stress occurs in 60% of the production areas globally (White and Casillo 1988). Navybean appears to exhibit at least as much isotopic variation as observed for other species. In a survey of 99 cultivars, Ehleringer et al. (1990) reported there was a range in Δ values under rainfed conditions of 3.2‰. In a subsequent study, substantial variation (more than 2.0‰) among a subset of 10 cultivars was observed, with Δ being positively correlated with leaf conductance to water vapour (Ehleringer 1990). Subsequent studies (Ehleringer et al. 1991) showed there was a significant negative correlation between Δ and WUE measured in contrasting genotypes in potted plants. Interestingly, cultivars developed for Central and South America had significantly higher WUE values (and lower Δ) than did lines developed for North America. Although the basis for the differences in WUE is unclear, it is thought that variations in leaf conductance or paraheliotropic leaf movements are involved.

In a recent report, White et al. (1991) have shown that a positive correlation between Δ and seed yield under rainfed conditions exists for Central and South American navybean cultivars. Interestingly, root length density and, presumably, soil-water extraction capability, was positively correlated with Δ (and WUE). These workers therefore suggest that selection for WUE, via low Δ, may be unproductive in navybeans, as unconscious selection for poor rooting capacity may occur. Thus, a negative association between WUE and ability to extract soil water (or T in Passioura's analysis) appears to exist in navybean, in a similar fashion to the negative association between WUE and HI in groundnut. As long as breeders are aware of these possible negative associations (which, it is to be hoped can be broken by genetic means), we suggest it is still important to pursue a selection program based on high WUE. Ultimately, the 'ideal' cultivar should have high levels of T, WUE and HI.

To summarise, it appears substantial cultivar variation in WUE exists in navybean, which could be potentially exploited using Δ as a surrogate for WUE. As for cowpea, definitive field studies aimed at verifying the correlation between WUE and Δ need to be conducted before Δ can be recommended as a selection trait. The extent of the apparent negative association between rooting

capacity and WUE also needs to be determined across a wider range of navybean germplasm.

*Soybean (*Glycine max *L.).* A large proportion of the area sown to soybeans in India, Australia and many other Southeast Asian countries is rainfed, yet soybeans are among the most sensitive of the grain legumes to water stress (Lawn and Byth 1979). Attempts to genetically manipulate performance under rainfed conditions have largely involved manipulation of phenology, particularly the use of short-duration genotypes. Some progress has been made using largely empirical selection procedures under rainfed conditions (Rose et al. 1992). Breeding for improved performance utilising reliable selection traits is currently being addressed in the ACIAR-funded project on soybean improvement in Thailand (Project No. 9040). Here, studies to establish the extent of soybean genotypic variation in physiological traits such as epidermal conductance, critical relative water content and osmotic adjustment are in progress (James et al. 1990).

There has been surprisingly little research done on genotypic variation in WUE and correlation with Δ in soybean. The only paper found reported that Δ is negatively correlated with biological nitrogen fixation in seven contrasting cultivars (Kumarasinghe et al. 1992). There have been no definitive reports as to the extent of cultivar variation in WUE in either pots or in the field, and whether Δ is negatively correlated with WUE. However, on the basis of the data of Kumarasinghe et al., it would seem there is considerable cultivar variation in Δ, as that report showed about a 1.5‰ difference between the extreme cultivars. Similarly, James (unpublished data) has found a 1% variation in Δ in a subset of soybean genotypes grown in the glasshouse. Clearly, glasshouse and field studies are urgently needed to assess the extent of WUE variation, and its correlation with Δ in soybean. Also, the existence of any correlation between WUE and SLA needs to be studied, as large cultivar differences in SLA (which have been correlated with leaf photosynthetic rate) are known to exist in soybean (Dornhoff and Shibles 1970, 1976).

*Chickpea (*Cicer arietinum *L.).* Chickpea is the third-most important of the world's legume crops, and is widely grown in India as a major source of protein. It is a cool season crop in the semi-arid and arid tropics, and because of its short growth cycle has the potential to fit into gaps in the cropping cycle. Scientists from Indian National Agricultural Research Systems believe drought reduces yield of chickpea by between 10–60% (ICRISAT 1991).

There are no published reports of genetic variation in WUE and its correlation with Δ in chickpea. However, following a recent field study in Queensland (Hammer, pers. comm) the crop is thought to have very low WUE. Therefore, glasshouse and field studies are needed to assess the extent of WUE variation and its correlation with Δ. Genotypic variation in leaf photosynthetic rate has been observed in chickpea, with SLA also being shown to be correlated with photosynthetic rate (Gupta et al. 1989). As a result, the existence of correlations between WUE and SLA in chickpea also needs to be addressed.

References

Briggs, L.J. and Shantz, H.L. 1913. The water requirements of plants. II. A review of the literature. USDA Bureau of Plant Industry Bulletin, 285, 1–96.

De Wit, C.T. 1958. Transpiration and crop yields. Versl. Landbrouwk. Orderz. 64.6. Institute of Biological and Chemical Research on Field Crops and Herbage, Wageningen, The Netherlands.

Dornhoff, G.M. and Shibles, R.M. 1970. Varietal differences in net photosynthesis of soybean leaves. Crop Science, 10, 42–45.

— 1976. Leaf morphology and anatomy in relation to CO_2 exchange rate of soybean leaves. Crop Science, 16, 377–81.

Ehleringer, J.R. 1990. Correlations between carbon isotope discrimination and leaf conductance to water vapour in common beans. Plant Physiology, 93, 1422–1425.

Ehleringer, J., Klassen, C., Clayton, C., Sherril, D., Fuller-Holbrook, M., Fu, Q. and Cooper, T.A. 1991. Carbon isotope discrimination and transpiration efficiency in common bean. Crop Science, 31, 1611–1615.

Ehleringer, J.R., White, J.W., Johnson, D.A. and Brick, M. 1990. Carbon isotope discrimination, photosynthetic gas exchange and transpiration efficiency in beans and range grasses. Oecologia, 11, 611–625.

Farquhar, G.D., Ehleringer, J.R. and Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology, 40, 503–537.

Farquhar, G.D. and Hubick, K.T. 1988. Water-use efficiency in legumes. Final review submission to ACIAR for Project 8407.

Farquhar, G.D., O'Leary, M.H. and Berry, J.A. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology, 9, 121–137.

Fischer, R.A. and Turner, N.C. 1978. Plant productivity

in the arid and semi-arid zones. Annual Review of Plant Physiology, 29, 277–317.

Ghorashy, S.R., Pendleton, J.W., Bernard, R.L. and Bauer, M.E. 1971. Effect of leaf pubescence on transpiration, photosynthetic rate and seed yield of three near-isogenic lines of soybeans. Crop Science, 11, 426–427.

Gupta, S.K., Bhatia, V.S., Singh, D.N. and Ganguly, S.B. 1989. Genotypic variation and relationship of specific leaf weight with photosynthesis (*Cicer arietinum* L.). Indian Journal of Plant Physiology, 32, 224–7.

Hall, A.E., Mutters, R.G. and Farquhar, G.D. 1992. Genotypic and drought induced differences in carbon isotope discrimination and gas exchange of cowpea. Crop Science, 32, 1–6.

Hall, A.E., Mutters, R.G., Hubick, K.T. and Farquhar, G.D. 1990. Genotypic differences in carbon isotope discrimination by cowpea under wet and dry field conditions. Crop Science, 30, 300–305.

Hall, A.E., Richards, R.A., Condon, A.G., Wright, G.C. and Farquhar, G.D. 1993. Carbon isotope discrimination and plant breeding. Plant Breeding Reviews, 11, (in press).

Hubick, K.T., Farquhar, G.D. and Shorter, R. 1986. Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut (*Arachis*) germplasm. Australian Journal of Plant Physiology, 13, 803–816.

Hubick, K.T., Shorter, R. and Farquhar, G.D. 1988. Heritability and genotype x environment interactions of carbon isotope discrimination and transpiration efficiency in peanut (*Arachis hypogaea* L.). Australian Journal of Plant Physiology, 15, 799–813.

Ismail, A.M. and Hall, A.E. 1992. Correlation between water-use efficiency and carbon isotope discrimination in diverse cowpea genotypes and isogenic lines. Crop Science, 32, 7–12.

James, A.T., Lawn, R.J., Ludlow, M.M. and Cooper, M. 1990. Genotypic variation in soybean for drought stress response. In Proceedings of 6th Australian Soybean Workshop. Brisbane, Queensland Department of Primary Industries.

Johnson, D.A., Richards, R.A. and Turner, N.C. 1983. Yield, water relations and surface reflectances of near-isogenic wheat lines differing in glaucousness. Crop Science, 23, 318–325.

Keatinge, J.D.H. and Cooper, P.J.M. 1983. Kabuli chickpea as a winter-sown crop in northern Syria: moisture relations and crop productivity. Journal of Agricultural Science, 100, 667–680.

Kirchhoff, W.R., Hall, A.E. and Thomson, W.W. 1989. Gas exchange, carbon isotope discrimination and chloroplast ultrastructure of a chlorophyll-deficient mutant of cowpea. Crop Science, 29, 109–115.

Kumarasinghe, K.S., Kirda, C., Mohamed, A.R.A.G., Zapata, F. and Danso, S.K.A. 1992. ^{13}C isotope discrimination correlates with biological nitrogen fixation in soybean (*Glycine max L.*). Plant and Soil, 139, 145–147.

Lawn, R.J. and Byth, D.E. 1979. Soybean. In: Lovett, J.V. and Lazenby, A. ed. Australian field crops. Angus and Robertson, Sydney, 198–231.

Markhart, A.H., III. 1985 Comparative water relations of *Phaseolus vulgaris* L. and *Phaseolus acutifolius* Gray. Plant Physiology, 77, 113–117.

Nageswara Rao, R.C. and Wright, G.C. 1994. Stability in the relationship between specific leaf area and carbon isotope discrimination across environments. Crop Science, 33, in press.

Richards, R.A. 1991. Crop improvement for temperate Australia: future opportunities. Field Crops Research, 26,141–169.

Rose, I.A., McWhirter, K.S. and Spurway, R.A. 1992. Identification of drought tolerance in early maturing indeterminate soybeans (*Glycine max* L.). Australian Journal of Agricultural Research, 43, 645–57.

Tanner, C.B. and Sinclair, T.R. 1983. Efficient water use in crop production: research or re-search? In: Taylor, H.M., Jordon, E.R. and Sinclair, T.R., ed., Limitations to efficient water use in crop production. American Society of Agronomy, Crop Science Society of American and Soil Science Society of America, 1–27.

White, J.W. and Castillo, J.A. 1988. Studies at CIAT on mechanisms of drought tolerance in bean. In: White, J.W., ed., Research on drought tolerance in bean. Cali, Colombia, Bean Program, CIAT.

White, J.W., Castillo, J.A. and Ehleringer, J.R. 1990. Associations between productivity, root growth and carbon isotope discrimination in *Phaseolus vulgaris* under water deficit. Australian Journal of Plant Physiology, 17, 189–98.

Wright, G.C., Hubick, K.T. and Farquhar, G.D. 1988. Discrimination in carbon isotopes of leaves correlates with water-use efficiency of field-grown peanut cultivars. Australian Journal of Plant Physiology, 15, 815–825.

— 1991. Physiological analysis of peanut cultivar response to timing and duration of drought stress. Australian Journal of Agricultural Research, 42, 453–70.

Wright, G.C., Hubick, K.T., Farquhar, G.D. and Nageswara Rao, R.C. 1992. Genetic and environmental variation in transpiration efficiency and its correlation with carbon isotope discrimination and specific leaf area in peanut. In: Ehleringer, J.R., Hall, A.E. and Farquhar, G.D., ed., Stable isotopes and plant carbon-water relatives. San Diego, Academic Press, 246–267.

Wright, G.C., Nageswara Rao, R.C. and Farquhar, G.D. 1994. Variation in water-use efficiency and carbon isotope discrimination in peanut cultivars under drought conditions in the field. Crop Science, 33, (in press).

Wright, G.C., Sarwanto, T.A., Rahmianna, A. and Syarifuddin, D. 1992. Investigation of drought tolerance traits conferring adaptation to drought stress in peanut. In: Wright, G.C. and Middleton, K.J., ed., Peanut improvement in Indonesia. ACIAR Proceedings 40, 74–84.

Carbon Isotope Discrimination, Water-Use Efficiency, Specific Leaf Area Relationships in Groundnut

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THE previous papers have demonstrated that extensive variation in WUE exists among groundnut cultivars. The difficulty in accurately measuring WUE in glasshouse and field situations, however, means it is virtually impossible to include such a trait into large-scale breeding programs. The pioneering work by Professor G. Farquhar and his colleagues (Farquhar et al. 1982) which showed that WUE and isotopic discrimination against ^{13}C during photosynthesis (Δ) were correlated, raised the possibility of using Δ as a rapid and non-destructive surrogate measure for selection of high WUE in large-scale breeding programs.

Subsequent research has further assessed the possibility of using Δ in groundnut breeding programs, by investigating the relationships between WUE and Δ under both glasshouse and field conditions. This paper reports the nature of these relationships. It is imperative that breeders and physiologists be confident that Δ is a reliable predictor of WUE before it can be recommended as a selection trait.

Theory for Associations between Carbon Isotope Discrimination and Water-use Efficiency

Atmospheric CO_2 contains two stable isotopes, ^{13}C and ^{12}C in a ratio of approximately 1:89. During photosynthesis, C_3 plants discriminate against $^{13}CO_2$ and take up less of it compared with $^{12}CO_2$ in relation to the proportions of these stable isotopes in the atmosphere. This discrimination has both physical and biochemical bases: slower diffusion of ^{13}C through the stomates, and lower affinity of the carboxylating enzymes for ^{13}C than ^{12}C (Farquhar et al. 1989). The degree of discrimination, Δ, is defined as:

$$\Delta = a + (b - a)p_i/p_a - d \qquad \ldots 1$$

where p_a and p_i are the intercellular and atmospheric vapour pressures for CO_2, and a, b, and d are parameters for isotope effects on discrimination, carboxylation, respiration and other processes [see Hubick et al. (1986) for details].

WUE is defined as the ratio of total dry matter (TDM) to transpiration (T) which can be modelled at many levels:

$$\text{WUE} = \frac{\text{TDM}}{\text{T}} = \frac{\text{A}}{\text{E}} = \frac{p_a(1 - p_i/p_a)}{1.6(e_i - e_a)} \qquad \ldots 2$$

Consequently, we can see from equations 1 and 2 that Δ and WUE are both a function of p_i/p_a. They will exhibit a negative, linear association providing p_a is relatively constant and $e_i - e_a$ does not vary (i.e. little variation in external humidity and leaf temperature). When Δ is measured on a carbon sample from a leaf, it provides a time and spatially integrated estimate of WUE.

Relationships in Groundnut

Groundnut cultivar variation in transpiration efficiency and correlation with Δ at the whole plant level

Using medium-sized pots (13 kg capacity) in a glasshouse study, Hubick et al. (1986) showed there was significant variation in WUE among seven *Arachis hypogaea* cultivars and two wild *Arachis* species, ranging from 1.41 to 2.29 g/kg. A close negative correlation (r^2= 0.66) between WUE and Δ was also observed, as expected on the basis of theory and data presented by Farquhar and Richards (1984) (Fig. 1). Differences in photosyn-

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thetic capacity were largely responsible for WUE variation, as dry matter production was negatively correlated with Δ, while water use showed no such relationship with Δ. The lack of a relationship between water use and Δ may be associated with the use of small pots in this study, where plants were forced to use most of the available water, and therefore ended up having the same total water use. Differing responses may occur in the field where access to soil water can be relatively unrestricted.

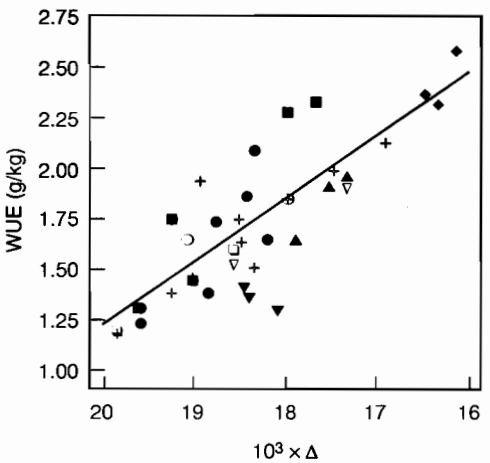

Figure 1. Transpiration efficiency versus carbon isotope discrimination (Δ) in a range of groundnut cultivars

The experimental confirmation that variation in WUE exists among groundnut cultivars, and that a strong relationship between WUE and Δ often exists under glasshouse conditions, suggest that Δ could be used as a criterion to exploit variation in WUE in breeding programs. There are, however, a number of potential sources of discrepancy between results from glasshouse plants in pots and plants grown under field conditions, including the following.

- There are difficulties in correctly apportioning water use into that lost by transpiration and that lost by evaporation. In field studies there are problems in estimating soil evaporation, in contrast to pots where it can be minimised (Turner 1986). Complications can also arise from differences between cultivars in the extent and timing of soil evaporation (Condon et al. 1991).
- There is generally a lack of data on root dry matter in field studies and WUE usually is based on above-ground dry matter. Differences among cultivars in apportioning of dry matter to roots and shoots may lead to erroneous comparisons of WUE defined on this basis. This error may be particularly large in severe drought conditions where total dry matter accumulation may be dominated by roots.
- The aerial environment of field canopies is characterised by complex interactions involving transfer of heat and water vapour, and the interactions are different from those around isolated potted plants. Reduced WUE of isolated plants that occurs because of reduced stomatal conductance may not necessarily be reflected at the canopy level, if the crop boundary layer conductance is relatively small (Cowan 1971, 1977, 1988; Jarvis and McNaughton 1985; Farquhar et al. 1989).

Definitive experiments aimed at assessing variation in WUE among groundnut cultivars, and the correlation between WUE and Δ therefore need to be conducted in canopies under field conditions. This information is essential in order to confirm that WUE variation exists under field conditions, and that Δ can be confidently used as a selection criterion for WUE. Also, this assessment needs to be conducted under both well-watered and water-limited conditions, as it has been shown that the correlation between WUE and Δ may break down under severe plant water deficits (Wright et al. 1992).

Groundnut cultivar variation in transpiration efficiency, and correlation with Δ in field canopies

Two large field experiments using a mini-lysimeter facility (Wright et al. 1988) were conducted to determine whether cultivar differences in WUE were occurring in small field canopies. One experiment was conducted under full irrigation (Wright et al. 1988), while the other imposed two levels of soil-water deficit (Wright et al. 1994). In both experiments WUE was measured only during the period between full canopy development (ca. 45 days after planting, DAP) and early podfilling (ca. 90 DAP). This was done to minimise the effects of soil evaporation, and avoid any confounding effects arising from maturity differences among cultivars.

The results from experiments clearly indicated that significant differences in WUE existed among groundnut cultivars in the field, under both water non-limiting, and limiting conditions (Table 1). In

general, variation in WUE among cultivars was associated with differences in dry matter accumulation rather than differences in transpiration. This result indicates that photosynthetic capacity, rather than leaf/canopy stomatal conductance, was dominating the WUE differences among groundnut cultivars.

Highly significant negative correlations were observed between Δ and WUE under both well-watered (r^2 = 0.67) and water-limited conditions (r^2 = 0.92) (Figs 2a and b). These relationships for field-grown groundnuts support the suitability of Δ as a selection criterion for screening for high WUE.

Changes in p_i/p_a, the ratio of internal CO_2 concentration in the leaf to ambient CO_2 concentration, and Δ can arise from changes in the balance between leaf stomatal conductance and photosynthetic capacity. Where p_i/p_a changes are due to stomatal movements, the relationship between WUE and Δ observed for well-ventilated, isolated leaves may break down in plants grown in canopies in the field because of significant canopy boundary layer resistances to fluxes of water vapour and heat (Cowan 1977, 1988; Farquhar et al. 1989). Where p_i/p_a changes in response to variation in photosynthetic capacity, the problem associated with weak coupling between the crop canopy and atmosphere is not as important, as increased p_i/p_a and Δ arise because of decreased assimilation rate, which causes a relatively small change in the CO_2 concentration in the air above the canopy and no effect on heat and vapour transfer through the boundary layer. The observation that total dry matter production (TDM) was negatively correlated with Δ for the groundnut cultivars examined in the field studies of Wright et al. (1988) and Wright et al. (1994) (Fig. 3) suggests that variation in photosynthetic capacity was the predominant source of variation in p_i/p_a (and therefore Δ).

Genotype × environment interaction and heritability for WUE and Δ

Genotype × environment interaction for WUE appears to be small in groundnut. Wright et al. (1988) found that although there were large differences in WUE and Δ in 'above-ground' as compared with 'in-ground' mini-lysimeters, cultivar ranking in these parameters was largely maintained across the two contrasting environments. Correlation coefficients (r) for WUE and Δ in 'in-ground' versus 'above-ground' mini-lysimeters were 0.91 and 0.83, respectively. Hubick et al. (1986, 1988) also reported that the ranking of WUE and Δ was consistent in a range of cultivars

Table 1. Dry matter (including roots), transpiration, WUE and Δ in groundnut cultivars grown in mini-lysimeters in field canopies under well-watered conditions (Wright et al. 1988) and two levels of water-limited conditions (Wright et al. 1994)

Study	Cultivar	Biomass (kg)	Water use (kg)	WUE (g/kg)	Δ (× 10^3)
Well-watered	Tifton-8	63.1	17.0	3.71	19.7
	VB-81	46.9	16.2	2.90	20.1
	Robut 33-1	55.3	19.0	2.91	20.8
	Shulamit	51.6	16.8	3.07	20.8
	McCubbin	48.6	16.9	2.88	20.8
	Cianjur	43.4	16.3	2.66	20.9
	Rangkasbitung	41.6	16.9	2.46	20.9
	Pidie	47.3	16.6	2.85	20.6
lsd P=0.05		7.0	1.5	0.3	0.55
Water limited	Tifton-8	37.5	12.2	3.07	19.4
(intermittent	Shulamit	35.7	12.8	2.79	19.9
stress)	McCubbin	36.3	13.4	2.71	20.7
	Chico	20.5	11.4	1.80	21.1
(terminal	Tifton-8	31.3	10.0	3.13	18.6
stress)	Shulamit	29.0	9.9	2.93	18.8
	McCubbin	26.8	10.0	2.68	19.4
	Chico	17.8	8.8	2.20	20.9
lsd P=0.05		5.61	1.90	0.38	0.93

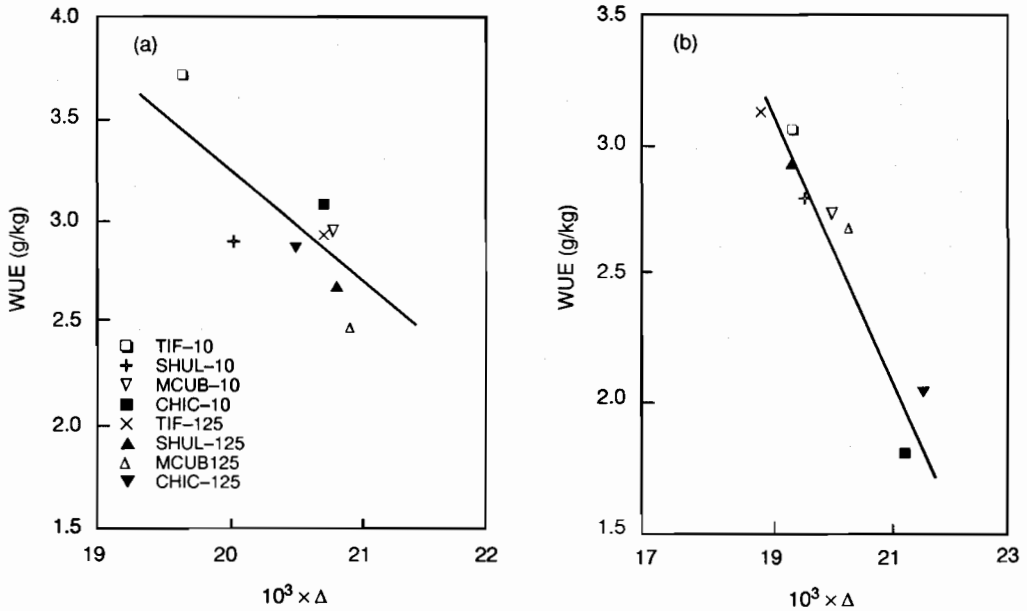

Figure 2. Relationship between water-use efficiency (WUE) and carbon isotope discrimination (Δ) under (a) well-watered and (b) droughted conditions for peanut cultivars grown in the field

under two contrasting water regimes in glasshouse studies. Hubick (1990) showed that although WUE and Δ varied significantly in response to watering

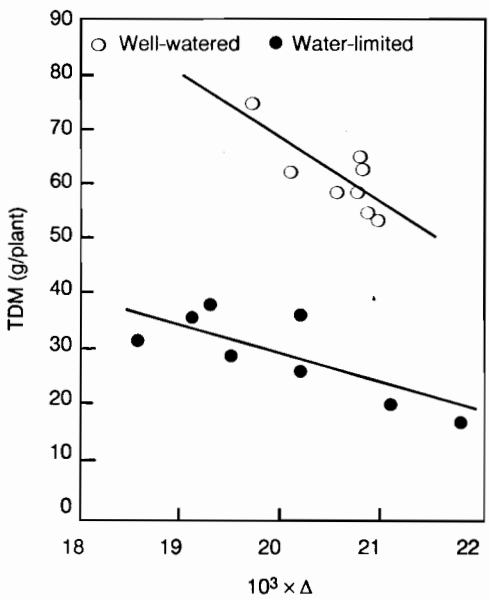

Figure 3. Total dry matter (TDM — roots and shoots) versus carbon isotope discrimination (Δ) in leaves of well-watered and water-limited groundnut cultivars growing in the field

treatment and source of nitrogen (mineral N versus nodule N), the ranking of WUE and Δ was similar under each treatment, again indicating there is low genotype × environment interaction for these parameters.

In 16 groundnut cultivars grown at 10 sites with widely different rainfall patterns in sub-tropical and tropical areas of Queensland, Australia, there was significant genotypic variation in Δ, with no significant interaction between genotype and environment (Hubick et al. 1988). The broad sense heritability (ratio of genotypic variance to the total, or phenotypic variance) or repeatability of Δ in this experiment was 81%.

Inheritance of Δ was studied in plants grown in pots using crosses of cultivars with contrasting Δ and WUE (Hubick et al. 1988). The F_1 progeny had Δ values similar to those of the low Δ cultivar, Tifton-8, and considerably smaller than those of Chico, the high Δ cultivar. This response suggests a degree of dominance for small Δ or large WUE in these genotypes. In the F_2 generation, the distribution of Δ exceeded the range between Tifton-8 and Chico, with two F_2 plants having smaller Δ values than those of the low Δ parent, Tifton-8 (Fig. 4). The F_2 distribution for Δ strongly suggested quantitative rather than qualitative inheritance for this trait.

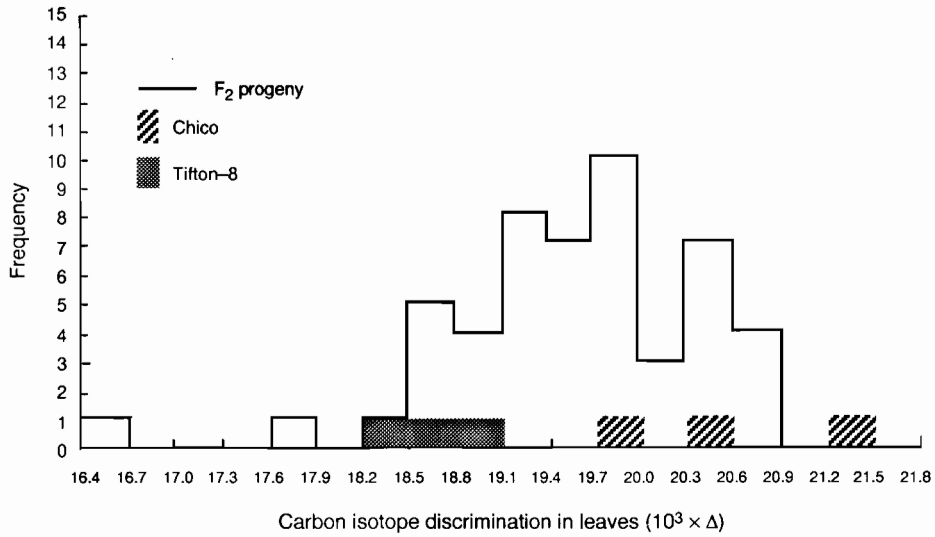

Figure 4. Frequency distribution of carbon dioxide discrimination (Δ) in leaves of well-watered plants of groundnut cultivars Tifton–8 and Chico, and their F_2 progeny, grown together in the same glasshouse environment

The results from the study of Hubick et al. (1988), in combination with the evidence we present here indicating that WUE and Δ have low genotype × environment interaction, suggest that effective selection for Δ, and hence W, could be conducted in a restricted number of environments. Indeed, the results indicate selection could possibly take place in a single environment, be it well-watered or water-limited, and in a glasshouse or field situation.

Relationships between specific leaf area, WUE and Δ

It has been observed over many experiments that specific leaf area (SLA, cm^2/g, which is negatively related to leaf thickness) is closely and negatively correlated with WUE, and also that SLA and Δ are positively correlated. Examples of the relationships between SLA and WUE, and SLA and Δ, measured in the mini-lysimeter study by Wright et al. (1994) are illustrated in Figures 5a and 5b. These observations are consistent with our earlier hypothesis that cultivars with high WUE have higher photosynthetic capacity. If it is assumed that the N:C ratio does not vary among cultivars then it is possible that those cultivars with thicker leaves had more photosynthetic machinery and the potential for greater assimilation per unit of leaf area. Indeed, Nageswara Rao and Wright (1994) have shown that specific leaf nitrogen (g N/m^2) is linearly related with SLA, such that thicker leaves had higher nitrogen contents (data not shown). Similar relationships between WUE and SLA, and Δ and SLA, have been reported elsewhere (Wright et al. 1988). A highly significant relationship between Δ and SLA was also observed for some 300 F_3 plants derived from a single cross of high and low Δ Indonesian cultivars grown in the field (Wright et al. 1992). Thus, there is considerable evidence to support the hypothesis that a very strong association between Δ and SLA exists. This finding has significant implications for breeding programs, where selection for WUE may be practised, as SLA is simple and inexpensive to measure, compared to the more expensive Δ measurement, which requires an isotope ratio mass spectrometer.

An experiment has recently been conducted to determine the generality of the SLA relationship with Δ by growing four cultivars with contrasting Δ in two contrasting temperature environments, under irrigated and rainfed conditions (Nageswara Rao and Wright 1994). The two sites, Kingaroy and Bundaberg, Australia, were similar except for their minimum night temperatures. Mean minimum temperatures during the season were 16°C at Kingaroy compared with 20°C at Bundaberg. Table 2 shows how environment, cultivar and watering regime all influenced the magnitude of SLA and Δ. For instance, SLA and Δ for each cultivar were significantly higher in the warmer

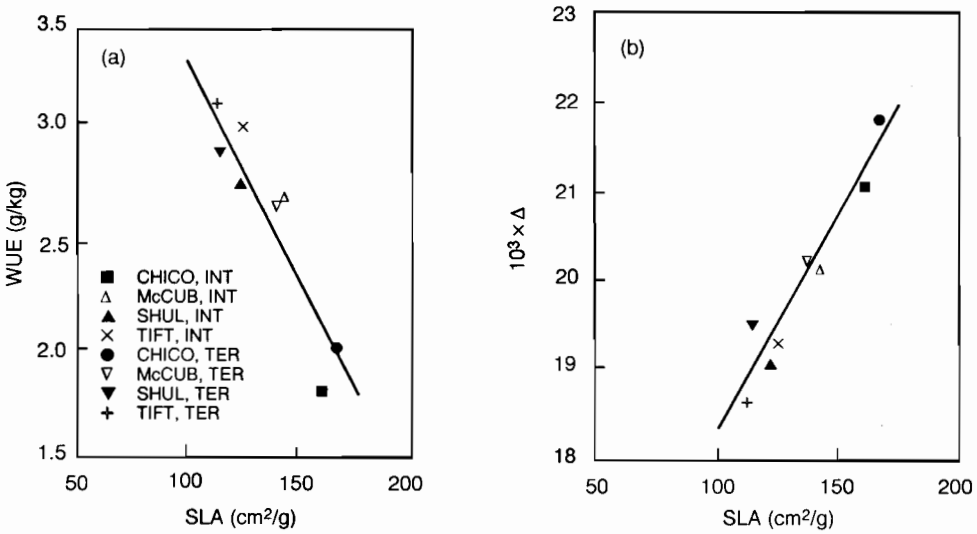

Figure 5. (a) Water-use efficiency (WUE) versus specific leaf area (SLA) and (b) carbon isotope discrimination (Δ) versus SLA for four groundnut cultivars grown under two levels of drought

Table 2. Specific leaf area (cm^2/g) and Δ (‰) measured at maturity for four groundnut cultivars grown at two sites (Bundaberg and Kingaroy) under two watering regimes (irrigated and rainfed).

Site	Treatment	Chico		McCubbin		Shulamit		Tifton	
		SLA	Δ	SLA	Δ	SLA	Δ	SLA	Δ
Kingaroy	Irrigated	155.2	22.44	145.9	21.17	124.0	21.24	117.7	20.40
	Rainfed	138.9	22.15	164.8	21.45	124.9	21.35	132.7	20.77
Bundaberg	Irrigated	184.9	23.21	174.2	22.68	166.8	22.97	148.3	21.50
	Rainfed	186.3	22.29	166.2	21.50	128.5	21.39	136.8	20.84

Bundaberg environment, while water deficits associated with the rainfed treatment tended to reduce SLA and Δ for each cultivar but not in Kingaroy. This effect was particularly apparent at Bundaberg where lower rainfall resulted in greater crop water deficits. The data clearly show that leaves of all cultivars became 'thicker' in response to low temperature and water deficits, possibly due to effects on leaf expansion and translocation of assimilate from the leaf (Bagnall et al. 1988). Of more interest, however, was the observation that cultivar ranking for SLA and Δ remained the same in each environment and watering regime. Indeed analysis of variance showed the main effects of location, irrigation treatments and cultivar were highly significant ($P < 0.05$) for SLA and Δ, while the genotype × environment interactions were non-significant. These results are consistent with the low genotype × environment interactions for WUE and Δ reported earlier.

The strong correlation between Δ and SLA reported previously (Fig. 5b) was again apparent for this data set (Fig. 6) even given the interactions noted above. Interestingly, the data from the contrasting temperature and water stress environment form a universal relationship. Even the data presented in Figure 5b, and other data we have measured elsewhere (e.g. Wright et al. 1992), fit well onto this relationship. The physiological mechanisms involved are unknown, and need further investigation. Nevertheless, the significant application of the relationship is obvious, in that breeders could use the inexpensively measured SLA in lieu of Δ to screen for high WUE among groundnut germplasm within particular environments.

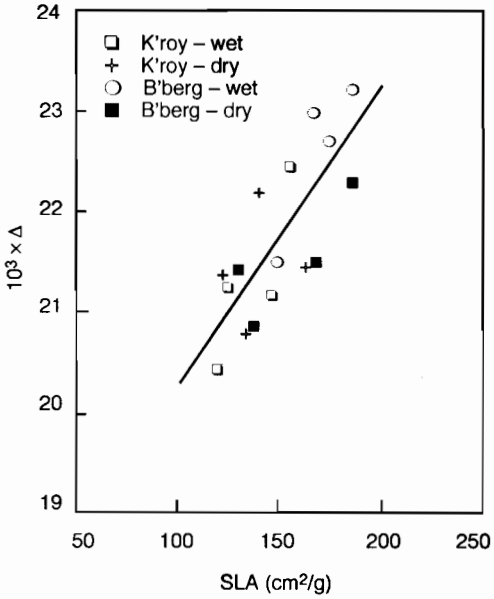

Figure 6. Carbon isotope discrimination (Δ) in leaves versus leaf area for four peanut cultivars grown in the field at Bundaberg and Kingaroy, Queensland, Australia

References

Bagnall, D.J., King, R.W. and Farquhar, G.D. 1988. Temperature dependent feedback inhibition of photosynthesis in peanut. Planta, 175, 348–354.

Condon, A., Dunin, F., Richards, R.A., Denmead, T., Leuning, R., De Pury, D., Wong, C. and Farquhar, G.D. 1991. Does a genotypic difference in stomatal conductance result in a difference in transpiration efficiency at the paddock scale. In: 31st Annual General Meeting of Australian Society of Plant Physiologists, Canberra, Australia, Abstract 42.

Cowan, I.R. 1971. The relative role of stomata in transpiration and assimilation. Planta, 97, 325–336.

Cowan, I.R. 1977. Water use in higher plants. In: McIntyre, A.K., ed., Water, planets, plants and people. Canberra, Australian Academy of Science, 77–107.

Cowan, I.R. 1988. Stomatal physiology and gas exchange in the field. In: Steffen, W.L. and Denmead, O.T. ed., Flow and transport in the natural environment: advances and application. New York, Springer-Verlag: 160–172.

Farquhar, G.D., Ehleringer, J.R. and Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology, 40, 503–537.

Farquhar, G.D., O'Leary, M.H. and Berry, J.A. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology, 9, 121–137.

Farquhar, G.D. and Richards, R.A. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat cultivars. Australian Journal of Plant Physiology, 11, 539–552.

Hubick, K.T. 1990. Effects of nitrogen source and water limitation on growth, transpiration efficiency and carbon-isotope discrimination in peanut cultivars. Australian Journal of Plant Physiology, 17, 413–430.

Hubick, K.T., Farquhar, G.D. and Shorter, R. (1986). Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut (*Arachis*) germplasm. Australian Journal of Plant Physiology, 13, 803–816.

Hubick, K.T., Shorter, R. and Farquhar, G.D. (1988). Heritability and genotype x environment interactions of carbon isotope discrimination and transpiration efficiency in peanut (*Arachis hypogaea* L.) Australian Journal of Plant Physiology, 15, 799–813.

Jarvis, P.G., and McNaughton, K.G. 1985. Stomatal control of transpiration scaling up from leaf to region. In: MacFadyen, A. and Ford, E.D., ed., Advances in ecological research. London Academic Press, 1–49.

Nageswara Rao, R.C. and Wright, G.C. 1994. Stability in the relationship between specific leaf area and carbon isotope discrimination across environments. Crop Science, 33, in press.

Turner, N.C. 1986. Crop water deficits. A decade of progress. Advances in Agronomy, 39,1–51.

Wright, G.C., Hubick, K.T. and Farquhar, G.D. 1988. Discrimination in carbon isotopes of leaves correlates with water-use efficiency of field-grown peanut cultivars. Australian Journal of Plant Physiology, 15, 815–825.

Wright, G.C., Hubick, K.T., Farquhar, G.D. and Nageswara Rao, R.C. 1992. Genetic and environmental variation in transpiration efficiency and its correlation with carbon isotope discrimination and specific leaf area in peanut. In: Ehleringer, J.R., Hall, A.E. and Farquhar, G.D., ed., Stable isotopes in plant carbon-water relations. San Diego, Academic Press, 246–267.

Wright, G.C., Nageswara Rao, R.C. and Farquhar, G.D. 1994. Variation in water-use efficiency and carbon isotope discrimination in peanut cultivars under drought conditions in the field. Crop Science, 33, in press.

Sampling Procedures for Carbon Isotope Discrimination and Specific Leaf Area in Groundnut

G.C. Wright*

To screen large numbers of lines for WUE would be extremely difficult because of the need to accurately measure both transpiration and total biomass (including roots) under glasshouse or field condition. This is no doubt the major reason why cultivar variation in WUE in a range of species has not been widely demonstrated, or pursued as a selection trait in breeding programs. For maximum effectiveness in developing cultivars with improved WUE, selection should be conducted in the large segregating heterogeneous populations that occur at various stages of a breeding program. Previous research on WUE in groundnut clearly indicates that carbon isotope discrimination (Δ) or SLA could be used to effectively select for WUE in large populations. This paper discusses some of the factors causing variation in Δ and SLA, as a prelude to defining optimal sampling techniques for use in the WUE project.

Factors Affecting Δ and SLA

Plant component

Hubick et al. (1986) found that Δ of all plant components was highly correlated with the Δ of leaf material. It is therefore considered that Δ in leaves should provide a reasonable guide to selecting groundnut cultivars for improved WUE.

Seasonal changes

The question of how early in a plant's life cycle Δ (or SLA) could be selected for and still represent its WUE characteristics is also pertinent in relation to selection in a breeding program. Figure 1 shows the temporal change in Δ at 4-day intervals until 54 days after emergence (and at maturity). It is clear that after about 15 days after emergence, Δ remains constant. A similar procedure (at 2-week intervals) was carried out for 4 cultivars in a field experiment under well-watered and droughted conditions (Wright et al. 1991). There was no significant interaction for Δ between irrigation treatment and time of sampling for the 4 cultivars. Based on these observations, the stability of Δ throughout crop ontogeny indicates that selection could take place very early during crop development.

Drought and temperature effects

Low night temperatures and crop-water deficits have both been shown to reduce the magnitude of Δ and SLA in a range of groundnut genotypes (see Table 2, page 57). Possible physiological reasons for these responses are discussed elsewhere (Nageswara Rao and Wright 1994). Importantly, there was little genotype × environment interaction for Δ or SLA, indicating that they are under strong genetic control.

Hall et al. (1993) cautioned that Δ may be different in plant material produced during stress periods, so sampling procedures would need to be developed to account for this effect. In terms of solely seeking improved WUE there may be an advantage in selecting for low Δ (or low SLA) under well-watered conditions, so as to minimise potential drought effects on Δ.

Canopy position

Canopy position has been shown to strongly influence Δ and SLA in leaves of groundnut. Recent data of Wright and Farquhar have demonstrated a linear decline in Δ and SLA from the top to the base of a fully developed canopy (cv. Tifton-8). Figure 2 illustrates this effect for Δ at two contrasting sites where minimum temperatures differed substantially. Similar trends have also been observed for SLA. It is clear from these data that canopy position has a marked effect on

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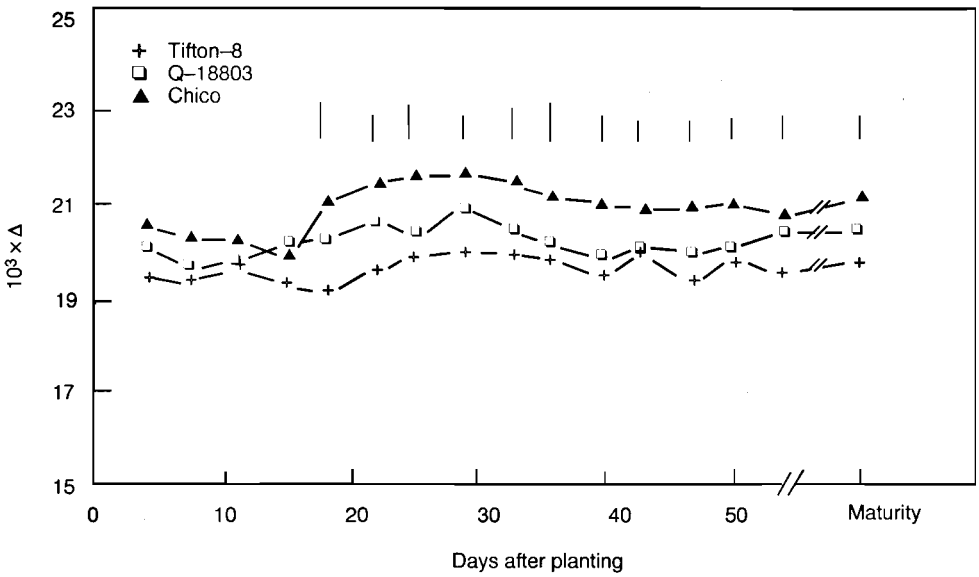


Figure 1. Changes in carbon isotope discrimination (Δ) in leaves with time for well-watered plants of cultivars Tifton–8, Q–18803 and Chico grown in a glasshouse. Bars denote lsd at $P < 0.05$.

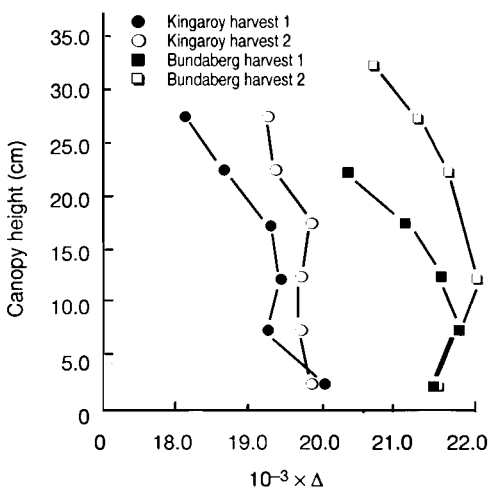


Figure 2. The change in carbon isotope discrimination (Δ) with canopy position for groundnut cultivar Tifton–8 grown at Kingaroy and Bundaberg, and harvested at 60 and 90 days after planting

Δ and SLA values, **within a genotype**. Thus, standardised sampling procedures will need to be employed in large-scale breeding programs to ensure this source of variation is minimised.

Conclusions

Based on the available information detailed above, it would seem the following sampling procedures should be used in order to minimise non-genetic variation in Δ and SLA measurements in the WUE project (and any future groundnut breedng program).

- Dried (80°C) leaf material should be used.
- It appears that sampling for Δ and SLA can be carried out at any stage of crop ontogeny, particularly under well-watered conditions. Under droughted conditions, breeders and physiologists will need to be aware that Δ (and SLA) may vary in genotypes as a result of differential water stress (e.g. due to differing length of season).
- Because canopy position can influence the magnitude of Δ and SLA it is suggested that only fully expanded sunlit leaves at the top of the canopy be sampled.

References

Hall, A.E., Richards, R.A., Condon, A.G., Wright, G.C. and Farquhar, G.D. 1993. Carbon isotope discrimination and plant breeding. Plant Breeding Reviews, 11, in press.

Hubick, K.T., Farquhar, G.D. and Shorter, R. 1986. Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut *(Arachis)* germplasm. Australian Journal of Plant Physiology, 13, 803–816.

Nageswara Rao, R.C. and Wright, G.C. 1994. Stability in the relationship between specific leaf area and carbon isotope discrimination across environments. Crop Science, 33, in press.

Wright, G.C., Hubick, K.T., and Farquhar, G.D. 1991. Physiological analysis of peanut cultivar response to timing and duration of drought stress. Australian Journal of Agricultural Research, 42, 453–70.

Growth Analysis Procedures for Estimating Growth Rates and Partitioning in Groundnut

R.C. Nageswara Rao*

WHILE genotype × environment interactions in groundnut pod yields have been reported by many researchers, it is not clear as to which growth parameter(s) were influenced by these interactions. Using a simple equation, pod yields (*Py*) in groundnut can be described as a function of $C \times D \times P$, where C is the crop growth rate, D the crop duration and P is partition coefficient (calculated as the ratio of pod growth rate and crop growth rate). In the current experiment, 50 entries have similar crop duration, so the variation in yield as influenced by the genotype and environment should be reflected in crop and pod growth rates and partitioning of the dry matter to pods. Analysis of crop growth during the growing season can help in explaining G × E interactions.

In the current project, six research centres representing a wide range of groundnut growing environments will be conducting the same field experiment. In such multilocation experiments, it is very important to follow a set of similar procedures in experimental layout, conduct of the experiment and data collection so that any treatment difference observed can be effectively interpreted. In this context, it is essential that we discuss and streamline the crop growth analysis procedures to be followed in the study so that uniform methodology is followed at all centres.

Plant Sampling for Growth Analysis

Plant sampling for growth analysis is done in several ways: random sampling of single plants from a plot, or harvesting a single or multiple row of given length, or harvesting plants from a given ground area, etc. Random sampling of single plants is not preferable for growth analysis in groundnut, particularly when experimental plots are small (such as is the case in the present experiment) because of significant compensation effects that could result due to removal neighbouring plants. For the purpose of the project it is suggested that three rows of 0.5 m length (0.45 m^2 ground area) be harvested after leaving one border plant from one end of the plot.

* ICRISAT, Andhra Pradesh, India.

Appendix

Technical Work Plan for Multi-location Studies on Water-use Efficiency in Groundnut

Objectives

- To examine genotypic variation for WUE and *p* under irrigated and drought conditions.
- To examine the role of WUE and *p* in drought tolerance under rainfed and simulated drought conditions.
- To examine the effect of G × E interactions on the interrelationship between WUE, carbon isotope composition (Δ), specific leaf area (SLA) and *p* in selected genotypes.
- To assess the losses due to drought at different locations in India, and scope for genotypic improvement.

Experimental Details

Statistical design: split plot

Main treatments:

T_1 Adequately irrigated condition. Replenish 100% of cumulative evaporation at 4-day intervals using drip system. Follow the examples for irrigation scheduling given in this manual.

Locations

Research station	University	Contact scientist	Address
Vridhachalam	Tamil Nadu Agricultural University	A. Arjunan	Regional Research Station, Vriddhachalam, Tamil Nadu 606 001
Tirupati	Andhra Pradesh Agricultural University	P.V. Reddy	Regional Agricultural Research Station, S.V. Agric. College Campus, Tirupati 517 502
ICRISAT	–	R.C.N. Rao	ICRISAT, Patancheru, Andhra Pradesh 502 324
Bangalore	University of Agricultural Sciences	M. Udaya Kumar/T.G. Prasad	University of Agricultural Sciences, Bangalore 560 065, Karnataka
Junagadh	National Research Centre for Groundnut/ Gujarat Agricultural University	Y.C. Joshi/P.C. Nautiyal	National Research Centre for Groundnut, P.B. No. 5, I.V. Nagar Road, Junagadh 362 001, Gujarat
Jalgaon	MPKV	Y.M. Shinde/S.S. Patil	Oilseeds Research Station, Jalgaon 425 001, Maharashtra
Durgapura	Rajasthan Agricultural University	S.N. Sharma/K.N. Sharma	Seed Technology Research Centre, Agricultural Research Station, Durgapura 302 018, Rajasthan

T_2 Simulated drought (a subset of 20 genotypes) under rain-out shelters (ROS) during 40-75 days after sowing. Irrigate with 25% of the cumulative evaporation at 4-day interval during the treatment period only. Follow the examples on irrigation scheduling given in this manual.

T_3 Rainfed treatment

Sub-treatments: For T_1 and T_3, 50 genotypes (48 genotypes to be supplied from ICRISAT and two local checks to be added by the scientists at their respective location).

For T_2, a subset of 20 genotypes from the above 50 are randomised separately (18 genotypes to be supplied from ICRISAT and two local checks to be added by the scientists at their respective locations).

Replications: 3

Plot size: 4 m length × 3 rows each genotype

Total experimental area required: See the field layout plan

Observations:

1. Daily meteorological data (please fill in the attached weather data sheets).
2. Time (days) for >50% emergence.
3. Time (days) for 50% flowering.
4. Light interception and growth sampling at 40, 75 and final harvest. Please follow the set procedures and fill the data formats.
5. Amount of water given to T1 and T2 treatments as per the procedure described in this manual.
6. Store the SLA samples from each harvest for carbon isotope composition analysis.
7. Soil analysis data (as per the enclosed soil data format).

Crop Management

1. Fertiliser: Fertilisers including gypsum and micro-nutrients will be applied as per the local recommendation.
2. Spacing: 30 cm × 10 cm (sow at 5 cm spacing between plants and then thin down to achieve required population).
3. Sowing depth: 5–7 cm.
4. Sowing time: On the onset of monsoon in 1993 (sowing dates may vary between locations).
5. Prophylactic measures for pests & diseases
   a) Seed treatment: Bavistin @ 2-3 g/kg seed
   b) White grub: Soil treatment with Phorate 10 G as per recommendation
   c) Sucking pests: Monocrotophos as recommended (sprays at regular intervals)
   d) Foliar fungal diseases: Chlorothalonil as recommended (sprays at regular intervals)
   e) Weeds: Hand weeding as required.

Irrigation Scheduling

For treatment 1 (irrigated):

Total plot area — 15.3 m × 15 m = 230 m^2

Full irrigation throughout the season, for situation where irrigation is given to replace potential evaporation measured from open pan (E_{pan}) i.e. 1 × E_{pan}.

Examples follow of how to calculate the volume of water to be applied at 4-day intervals, in the presence and absence of rainfall.

Example 1:

Day no.	Daily E_{pan} (mm)	Rain (mm)	Cumulative E_{pan} (mm)	Remarks
1	4.0	–	4.0	
2	4.5	–	9.5	
3	4.5	–	14.0	
4	6.0	–	20.0	To apply 20 mm of irrigation, apply 4600 litres for 230 m^2 plot (20 mm × 230 m^2 = 4600 L)
5	6.5	–	6.5	
6	5.3	–	11.8	
7	4.2	20	16.0	
8	7.2	–	23.2	In case of some rain not exceeding the cumulative E_{pan} within 4-day period, irrigate with 23.2–20 mm = 3.2 mm, i.e. 3.2 mm × 230 L = 736 L for 230 m^2 plot

Example 2:

If rainfall in any 4-day period exceeds 25 mm, do not irrigate. Start cumulative E_{pan} calculation from 5th day (day 1 for second cycle of irrigation) to 8th day.

Day no.	Daily E_{pan} (mm)	Rain (mm)	Cumulative E_{pan} (mm)	Remarks
1	5.1	–	5.1	
2	4.8	20	9.9	
3	6.1	10	16.0	
4	5.8	–	21.8	Rainfall > 25 mm no irrigation
5	5.3	–	5.3	
6	6.1	–	11.4	
7	7.1	–	18.5	
8	6.3	–	24.8	Irrigate with 24.8 mm × 230 L = 5704 L

Example 3: Irrigation scheduling for treatment 3 (rain-out shelter — ROS)

Total plot area = 7.2 m × 15 m = 108 m^2

Until day 40, irrigate ROS treatment similar to that of T_1 (i.e., no need to cover with ROS), From day 40 until day 75, irrigate at 4-day intervals at 25% of E_{pan} and cover with ROS as needed.

Day no.	Daily E_{pan} (mm)	Rain (mm)	Cumulative E_{pan} (mm)	Remarks
1	6.1	-	6.1	
2	5.0	-	11.1	
3	5.3	-	16.4	
4	6.1	-	22.5	Irrigate with 25% of E_{pan} i.e. 22.5 × 0.25 × 108 = 608 L

Sampling Procedure for SLA and Δ

SLA measurements are to be made at each growth analysis harvest; i.e. 40, 75, and final harvest.

1. From each plot, sample 20 fully expanded 3rd or 4th leaf (from main stem apex) from randomly selected plants. Separate leaflets and discard petioles.
2. Measure leaf area of 80 leaflets.
3. Oven dry the leaflets.
4. Weigh the dried leaflets (up to 2 decimal places) and enter the data in columns C3 and C4 in Growth Data format I.
5. Store the dried leaflets in paper bags for later analysis. Label the bags to indicate harvest date, replication, treatment and plot number.

Radiation Interception

The amount of solar radiation intercepted by a crop canopy is an important parameter determining the radiation-use efficiency of the crop.

The fractional amount of solar radiation absorbed by a crop canopy at a given time can be determined as:

$$LI\ (\%) = [(R_a - R_b)/R_a] \times 100$$

where,

LI = radiation interception (%)
R_a = incident irradiance (above the canopy)
R_b = radiation at the soil surface below the canopy

Procedure:

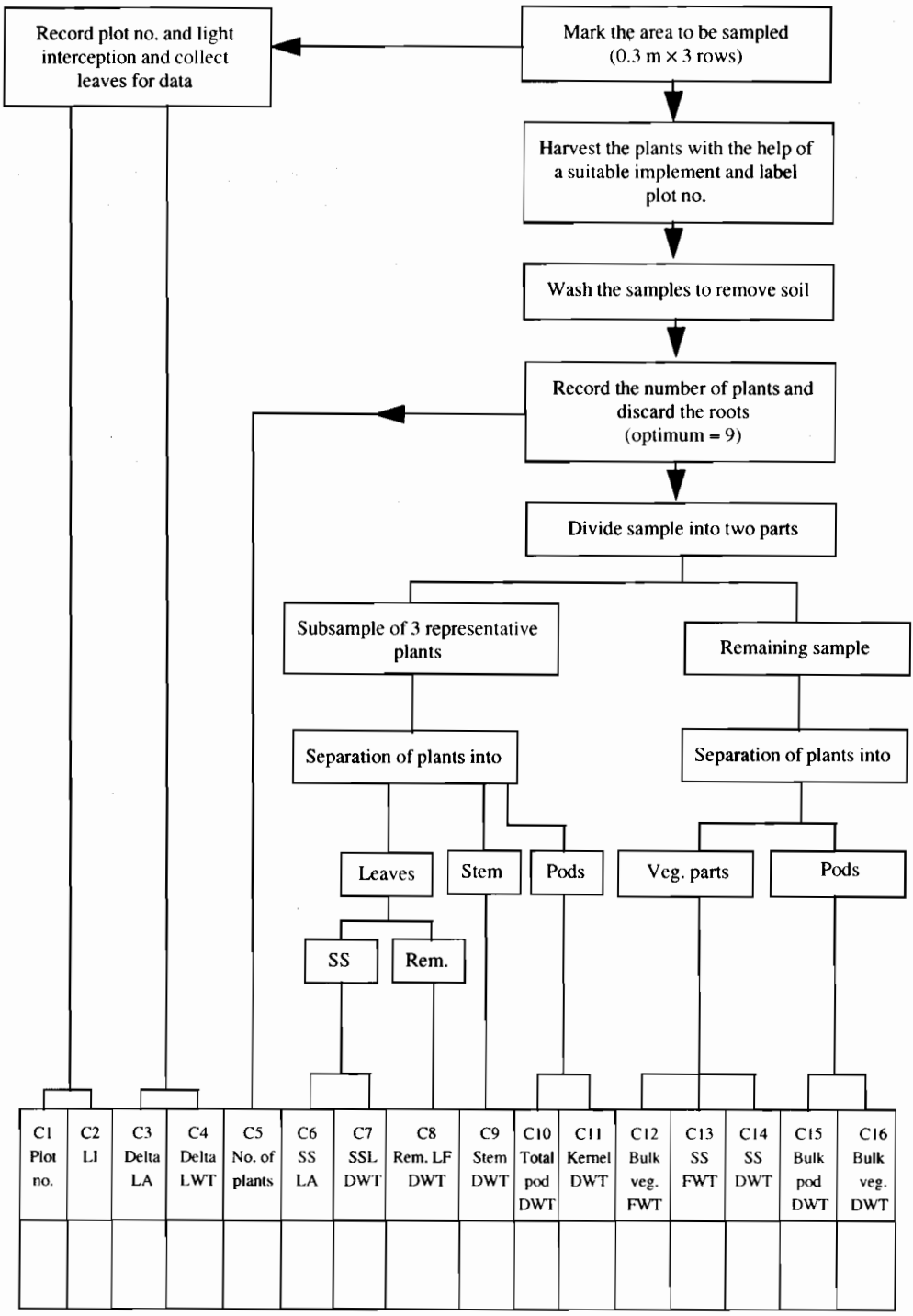
1. Always record LI during the middle of the day when the sun is at its zenith. Avoid days with variable cloud cover. Sunny days are the best to make the measurements.
2. Keep the solarimeter in the sun for 10 minutes to warm up.
3. Connect the +ve and -ve terminals of the solarimeter to the millivolt recorder.
4. Keep the solarimeter above the canopy at a horizontal level with the panel facing the sky. Record R_a from the millivolt meter.
5. Record the radiation received at the soil surface by placing the solarimeter on the soil surface below the canopy, perpendicular to the rows.
6. Record R_a and R_b in C2 column of the Growth Data format I

Calibration of solarimeter to estimate amount of radiation interception: Procedure for calibration will be circulated separately before the end of the season.

Flow Chart for Growth Analysis

The flow chart on the next page shows the sequence of steps to be followed in processing plants and in data collection. It is also important to record data in a fixed format for the convenience of verification or data analysis.

Flow Chart for Growth Analysis of Groundnut



Key: LI, light interception; SS, subsample; LA, leaf area; SSL, subsample leaf; DWT = dry weight, Rem LF, remaining leaf; Veg., vegetative.

Technical Work Plan for University of Agricultural Sciences, Bangalore*

A. Groundnut

I. Field experiments (July–Nov. 1993)

Variation in groundnut genotypes for WUE and partitioning under drought conditions (similar to multi-location experiment).

Main-treatments

Irrigation regimes:

T_1 = adequately irrigated
T_2 = simulated drought under ROS
T_3 = rainfed

Sub-treatments

Genotypes: 50 for T_1 and T_3 treatments a subset of 20 genotypes for T_2.

Layout and randomisation will be followed as described for other locations during the WUE methodology workshop at ICRISAT.

Observations

A. Climate and crop growth

1. Daily meteorological data
2. Time to 50% emergence
3. Time to 50% flowering
4. Light interception, leaf sampling for SLA and Δ, and growth analysis at 40, 75 days after sowing and final harvest.
5. Amount of water supplied in T_1 and T_3 treatments.

B. Soil moisture

In three selected genotypes, changes in soil moisture content during the treatment period will be monitored at various depths up to 3 m, in T_1 and T_2, using a neutron probe scanner.

3 geno × 2 tubes per plot × 3 reps × 2 treatments = 36 tubes

C. Carboxylation efficiency

In six selected genotypes with variable SLA, the following observations will be collected at 40 and 75 DAS in treatments T_1 and T_2 only.

- gas exchange
- leaf protein content
- RuBisCO content

Using these primary values, the following will be computed.

(i) A/gs (ii) A/Ci
(iii) A/RuBisCO (iv) RuBisCO/Protein

II. Pot culture experiment (July–Nov. 1993)

Container studies of water-use efficiency.

Treatments

Genotypes	:	8
Replication	:	6
Growth stages during which WUE is measured	:	a. 30–65 DAS b. 65–100 DAS
Irrigation levels	:	2–a. 100% field capacity 2–b. 50% field capacity
Pot size	:	Medium (to hold 20 kg soil)
No. of pots	:	250 pots

Observations

- Total cumulative water added
- Biomass accumulated during experimental period (including roots)
- Leaf area development
- Partitioning

Leaf samples will be collected (3rd fully expanded leaf) on 70 and 90 DAS for SLA and Δ.

Gas exchange parameters and carboxylation efficiency

- Gas exchange parameters
- Leaf protein and RuBisCO content

* Abbreviations: SLA = specific leaf area; Δ = carbon isotope discrimination; WUE = water-use efficiency; RuBisCO = ribulose 1–5 biphosphate carboxylase; A = carbon assimilation rate; g_s = stomatal conductance; c_i = partial pressure of CO_2 in leaves; DM = dry matter; LA = leaf area; E_{pan} = evaporation measured on open pan (class A type).

B. Chickpea

Initial screening of chickpea genotypes for Δ will be done in the leaf samples of 40 genotypes collected at ICRISAT during the 1992–93 season. About 8 genotypes representing extreme variation in Δ and partitioning will be selected for use in the detailed studies.

I. Pot culture experiment — basic studies (Nov.–Mar. 1993–94)

Treatments

Genotypes	:	10 (ICRISAT to supply seeds)
Replications	:	6
Growth stages during which WUE is measured	:	2 – a. 30–65 DAS 2 – b. 60–90 DAS
Irrigation levels	:	2 – a. 100% FC 2 – b. 50% FC

Details are as described for the groundnut pot culture experiment.

II. Lysimeter experiment in field (Oct.–Feb. 1994–95)

Treatments

Genotypes	:	5 nos (4 rows each)
Irrigation	:	T_1 – Adequate irrigation T_1 – Maintaining at 25% E_{pan} from 40 to 75 DAS
Replications	:	3 nos (3 ROS)
	:	2 lysimeters per replication per genotype as shown (enclosed) in the field layout plan.
Observations I	:	a. Daily meteorological data b. Initial DM/LA (at 40 DAS) c. Final DM/LA at 75 DAS d. Root biomass e. SLA and at 40 and 75 DAS
Observations I I	:	a. Total biomass observations from bulk area adjacent to lysimeter

C. Cowpea

I. Field experiment — initial screening for SLA and Δ (Jul.–Nov. 1993)

Treatments

Genotypes	:	100
Replications	:	3

Each genotype will be raised in one row of 5 m length in three replications.

Leaf samples (3rd fully expanded leaf) will be collected for SLA and Δ. Samples will be sent to Dr G.D. Farquhar, ANU, for Δ analysis.

Observations	:	Total dry matter at harvest and pod yield.

II. Pot culture experiments – basic studies (Jul.–Nov. 1994)

Treatments

Genotypes	:	10-15
Replications	:	6
Growth stages during which WUE is measured	:	2–a. 30–60 DAS 2–b. 60–95 DAS
Irrigation levels	:	2–a. 100% FC 2–b. 50% FC

Other details are as described for groundnut pot culture experiment.

III. Lysimeter experiment in field (Jul.–Nov. 1995)

Mini-lysimeters studies using contrasting lines (JASON 1995).

Treatment and observations details similar to the experiment suggested for chickpea.

Summary of Work Plan

Crop	1993–94	1994–95	1995–96
Groundnut	July–Nov. Field and pot experiments	–	–
Chickpea	Nov.–Feb. Pot experiment with 10 genotypes ONDJ Seed multiplication	Nov.–Feb. Mini-lysimeter experiment	Nov.–Feb. Mini-lysimeter experiment repeat
Cowpea	July–Nov. Germplasm (100 genotypes) screening for Δ in field experiment	July–Nov. Pot experiment with 8 selected genotypes JASON Mini-lysimeter experiment	

Summary of Activities

Activity		1993–94	1994–95	1995–96
A. Work plan at Tirupati, Jalgaon, Durgapura and ICRISAT centres for the groundnut experiment.				
1. Evaluation of germplasm for WUE		July–Nov.	July–Nov.	July–Nov.
2. Compilation of data		Dec.	Dec.	Dec.
3. Dispatch of complete data book		Jan.	Jan.	Jan.
B. Work plan at Vriddachalam and Junagadh centres for the groundnut experiment.				
1. Evaluation of germplasm for WUE	(Rainy)	July–Nov.	July–Nov.	July–Nov.
	(Post-rainy)	Jan.–May	Jan.–May	Jan.–May
2. Compilation of data	(Rainy)	Dec.	Dec.	Dec.
	(Post-rainy)	Jun.	Jun.	Jun.
3. Dispatch of complete data book	(Rainy)	Jan.	Jan.	Jan.
	(Post-rainy)	Jul.	Jul.	Jul.
C. Work plan at UAS, Bangalore for the groundnut experiment				
1. Evaluation of germplasm for WUE		July–Nov.		
2. Pot experiment with 6 selected genotypes		July–Nov.		
3. Compilation of data		Dec.		
4. Dispatch of data book		Jan.		