Shade Tolerance of Tropical Forages: A Review

C. C. Wong*

Abstract

The paper reviews the shade tolerance of tropical forages and discusses the adaptation of species to low light. Shading reduces tiller production and leaf, stem, stubble and root yield but increases specific leaf area and shoot/root and leaf/stem ratios, particularly in shade-tolerant species. Yield responses of many tropical forages to shading reflected the strong relationship between productivity and irradiance, but was often confounded with nitrogen availability.

There is potential for improvement of forage productivity in light to moderate shade but less in dense shade where yields of both high-yielding shade-intolerant plants and low-yielding shade-tolerant plants are similar and low. However, the ability of shade-tolerant plants to persist under shade and regular defoliation may be of greater importance for long-term productivity. A number of species suitable for various shade environments is reported. Species suitable for light to moderate shade are *Brachiaria decumbens, Brachiaria brizantha, Panicum maximum, Centrosema pubescens. Desmodium intortum* cv. Greenleaf, *Leucaena leucocephala, Calopogonium caeruleum, Pueraria phaseoloides* and *Desmodium ovalifolium.* In dense shade (<30% sunlight) *Axonopus compressus. Brachiaria miliiformis, Paspalum conjugatum* and *Stenotaphrum secundatum* persisted well but had a low productivity. The significance of persistence in shade-tolerant forages for long-term productivity in dense shade was emphasised.

THE plantation crops of southeast Asia and the South Pacific cover an extensive area, including at least 5 million ha of coconut plantation in Indonesia, Philippines and South Pacific islands, and another 2.8 million ha of rubber and oil palm in Malaysia (Rika 1985). These plantation lands with their understorey forages represent one of the most extensive and underutilised feed resources in the region.

The major constraint in the exploitation of these plantation lands for forage and ruminant production is the fast-changing light environment below the plantation canopy over time. Shade-tolerant species are needed to improve and sustain production. This paper reviews both indigenous and improved tropical forages for their shade tolerance and forage productivity in plantation crops.

Shade Tolerance

Currently, there is no acceptable definition of shade tolerance but it may best be defined, agronomically, as the relative growth performance of plants in shade compared to that in full sunlight as influenced by regular defoliation. It embodies the attributes of both dry matter (DM) productivity and persistence. The reported shade tolerance of some common tropical forages is illustrated in Table 1.

Morphological Adaptation

Shade affects the growth and morphological development of plants. Tiller production and leaf, stem, stubble, and root production are often reduced at low light with formation of thinner leaves with higher water content and a higher specific leaf area (Wong et al. 1985a,b). The increased partitioning of DM to the leaf component at the expense of root often results in higher shoot/root, leaf/stem, leaf weight and leaf area ratios, especially in grasses (Table 2). Grasses with high shade tolerance were found to have a higher specific leaf area and leaf area ratio than those with low shade tolerance (Table 3). The same trend was to a lesser extent observed with legumes (Table 3).

Morphological acclimatisation of forages to light attenuation is an adaptive strategy to compensate, at least partially, for the lower photosynthetic rate per unit leaf area. In addition, chemical changes may also occur under low light to enhance photosynthetic efficiency. Foliar nitrogen has been shown to increase in shaded grasses but not in shaded legumes (Wong and Wilson 1980; Samarakoon 1987). Higher nitrogen concentrations in grass leaves was associated with enhanced efficiency of conversion of radiant energy

*Livestock Research Division, MARDI, Malaysia

Table 1. Shade tolerance of some important tropical forages.

Shade tolerance	Grasses	Legumes
High	*Axonopus compressus* *Brachiaria miliiformis* *Ischaemum aristatum* *Ottochloa nodosa* *Paspalum conjugatum* *Stenotaphrum secundatum*	*Calopogonium caeruleum* *Desmodium heterophyllum* *Desmodium ovalifolium* *Flemengia congesta*
Medium	*Brachiaria brizantha* *Brachiaria decumbens* *Brachiaria humidicola* *Digitaria setivalva* *lmperata cylindrica* *Panicum maximum* *Pennisetum purpureum* *Setaria sphacelata*	*Calopogonium mucunoides* *Centrosema pubescens* *Desmodium triflorum* *Pueraria phaseoloides* *Desmodium intortum* *Leucaena leucocephala*
Low	*Brachiaria mutica* *Cynodon plectostachyus* *Digitaria decumhens* *Digitaria pentzii*	*Stylosanthes hamata* *Stylosanthes guianensis* *Zornia diphylla* *Macroptilium atropurpureum*

Source: adapted and modified from Shelton et al. 1987, Reynolds 1978, Eriksen and Whitney 1982, Chen and Bong 1983, and Wong et al. 1985b.

Table 2. Growth characteristics of tropical grasses and legumes grown at four light levels (mean of 12 species).

Light level (% PAR)	Tillers (no./pot)	LWR	LAR (cm^2/g)	Leaf/Stem ratio	Shoot/root ratio	SLA (cm^2/g)	Foliar nitrogen (%)
Grasses							
100	132	0.32	0.4	1.1	2.5	170	1.44
56	92	0.38	0.6	1.2	3.8	227	1.74
34	63	0.49	1.2	1.6	7.1	332	2.07
18	27	0.51	1.3	1.8	6.7	354	2.33
Legumes							
100	153	0.47	1.1	1.2	6.5	227	3.46
56	132	0.48	1.5	1.2	8.6	301	3.52
34	53	0.49	1.9	1.2	14.9	378	3.81
18	36	0.50	2.0	1.2	14.2	391	3.78

LWR = leaf weight ratio, LAR = leaf area ratio, SLA = specific leaf area

(Sophanodora 1989). On the other hand, nodulation in shaded legumes was adversely affected and nodule numbers declined with increasing shade intensity, and this may explain the contrasting response in legumes.

Yield Response to Shade

Shade imposes a limitation to biological productivity in plants although the extent of the limitation varies with shade tolerance of the species and the nitrogen supply.

Eriksen and Whitney (1981) found that in high-yielding grass species, well supplied with nitrogen, yield increased almost linearly with increasing light up to 75% of full sun, and then tended to plateau as light transmission increased to 100% of full sun (Table 4). At low nitrogen, yield of the same species maximised at lower light levels. Wong et al. (1985a) obtained similar results with high-yielding species well supplied with nitrogen, indicating that light was not the only factor controlling yield. Nevertheless, for species reputed to be shade-tolerant *(Axonopus compressus* and *Paspalum conjugatum)* (Table 2), yield maximised at much lower

Table 3. Percentage composition of plant parts, specific leaf area and leaf area ratio of some tropical forages grown in shade (mean of 64. 30. 18 and 9% light transmission).

Species	Composition (% of DM)			SLA cm^2/g	LAR cm^2/g
	Root	Stem	Leaf		
High shade tolerance					
Paspalum conjugatum	13	47	40	342	1.1
Axonopus compressus	24	30	46	296	1.2
Desmodium ovalifolium	11	37	52	437	2.3
Calopogonium caeruleum	12	35	53	407	2.2
Medium shade tolerance					
Panicum maximum	21	28	52	211	0.8
Digitaria setivalva	21	24	56	248	0.6
Centrosema pubescens	13	37	50	388	2.0
Low shade tolerance					
Digitaria decumbens cv. Transvale	13	5	30	176	0.4
Stylosanthes guianensis cv. Schofield	8	49	43	284	1.2
Stylosanthes hamata cv. Verano	12	41	48	222	1.7

SLA = specific leaf area, LAR = leaf area ratio
Source: Wong et al. 1985a,b

light levels (Table 4). It can be concluded from these data that both potentially high-yielding species, which are limited by nitrogen availability, and low-yielding shade-tolerant species, are light-saturated at low levels of solar radiation.

An unusual effect of shade on growth of grasses has been reported by Wilson et al. (1990). The DM and nitrogen yield of a *Paspalum notatum* pasture was higher under a *Eucalyptus grandis* plantation than in the adjacent full sun area. The authors suggested that shade may have had a positive effect on the availability of soil nitrogen (Wilson et al. 1990).

Legumes behaved differently in the studies by Wong et al. (1985b) and Eriksen and Whitney (1982) (Table 4). While in the experiment by Eriksen and Whitney (1982) the response of legume yield to light transmission was close to linear, most species showed maximum yield at low light level in the experiment by Wong et al. (1985). No clear response patterns can therefore be claimed.

For both grasses and legumes, species differences were greater under moderate to high light transmission than under low light. The low yield potential of all species in low light remains a major constraint to forage productivity in plantations which close their canopies with age. However, in plantations with open canopies such as coconut, species with medium shade tolerance can be exploited to obtain higher yields.

The most productive species for moderate shade, from the work of Wong et al. (1985b) and Eriksen and Whitney (1982), were *Panicum maximum, Brachiaria brizantha, Brachiaria decumbens* and *Desmodium intortum.* For low light environments, the more shade-tolerant species *Axonopus compressus* and *Paspalum conjugatum* were not highly productive but were persistent.

The productivity of some promising forages grown under natural plantation shade is shown in Table 5. It is in the dense shade that productivity of shade-tolerant species has been disappointing. At light levels of less than 25% sunlight, there appears to be no superiority of any particular forage. Many introduced species died out in dense shade (Chen and Bong 1983; Chen and Othman 1984) and weed invasion was often as high (Mohd Najib 1989; Wong et al. 1988). The potential to use improved pastures at such low light levels to increase forage production therefore remains doubtful (Wilson 1988).

Persistence

However, an important character in the selection of shade-tolerant species is their ability to persist and compete with the shade-tolerant weeds under continual defoliation or herbivory. The term persistence includes both the survival of individual plants (longevity and vegetative propagation) and seedling replacement. Indigenous shade species such as *A. compressus, S. secundatum, B. miliiformis* and *P. conjugatum* have been the most persistent and productive under low light levels. Any new shade-tolerant genotypes that are identified must be able to out-perform these species in dense shade.

Table 4. Productivity (DM t/ha/yr) of some tropical forages in pure swards under artificial shade of varying irradiance.

Species	Shade level (% sunlight)				Reference
	18-27	34–45	60–70	100	
(a) Grasses					
0 N/ha/yr					
Brachiaria brizantha	12	13	12	13	Eriksen and Whitney (1981)
Brachiaria miliiformis	9	8	7	4	
Digitaria decumbens	6	114	10	9	
Panicum maximum	13	15	12	9	
Pennisetum clandestinum	5	9	9	4	
365 kg N/ha/yr					
Brachiaria brizantha	15	21	30	29	Eriksen and Whitney (1981)
Brachiaria miliiformis	14	20	24	18	
Digitaria decumbens	10	20	25	29	
Panicum maximum	14	24	32	30	
Pennisetum clandestinum	8	10	20	16	
150 kg N/ha/yr					
Axonopus compressus	3	8	7	4	Wong et al. (1985a)
Brachiaria decumbens	8	13	16	23	
Panicum maximum	8	16	16	22	
Setaria sphacelata cv. Kazungula	6	10	14	12	
Paspalum conjugatum	3	4	4	4	
(b) Legumes					
Calopogonium caeruleum	2	4	4	3	Wong et al. (1985b)
Centrosema pubescens	1	2	2	4	
Desmodium ovalifolium	4	5	5	4	
Stylosanthes guianensis cv. Endeavour	5	7	9	15	
Pueraria phaseoloidies	2	3	3	4	
Desmodium intortum cv. Greenleaf	9	15	19	20	Eriksen and Whitney (1982)
Centrosema pubescens	6	9	12	14	
Macroptilium atropurpureum	3	5	9	13	
Stylosanthes guianensis cv. Schofield	3	5	12	17	

Persistence of forages is affected not only by their tolerance to shading but also by their ability to tolerate regular defoliation. A longer cutting interval has enhanced persistence of a number of grasses grown under the closed canopy of oil palms (Table 6). The shade-tolerant species *Axonopus compressus* and *Paspalum conjugatum* (Table 1) had a higher plant density at the end of the experiment than at the beginning, while less shade-tolerant grasses persisted poorly. This may have been related to either poor shade tolerance or damage from pests and fungal diseases in dense shade. The persistence of legumes under the closed canopy of oil palms was, with the exception of *Calopogonium mucunoides*, generally poor in a trial reported by Chen and Othman (1984).

In other trials the sown grasses and legumes *Brachiaria decumbens, Brachiaria mutica, Brachiaria humidicola, Centrosema pubescens* and *Calopogonium mucunoides* did not persist under regular grazing (Chen et al. 1978, Smith and Whiteman 1985). Ultimately they were replaced by naturalised species of lower productivity.

Identification of characteristics of shade-tolerant species, that render them persistent under frequent defoliation, may help our understanding of stability of forages in integrated plantation production systems and lead to more rational species evaluation procedures for shade tolerance.

Conclusions

The performance of tropical forages under shade, including shade-tolerant species such as *Axonopus compressus, Paspalum conjugatum, Desmodium heterophyllum* and *Stenotaphrum secundatum*, is poor in low light (<25% of full sunlight). There is a need for more productive shade-tolerant species.

At higher light levels such as in mature coconut plantations (50-80% light transmission), and during the early establishment of rubber and oil palm plantations, improved tropical grasses and legumes,

Table 5. Productivity (DM t/ha/yr) of some tropical forages in pure swards grown under the natural shade of plantation crops.

Species	Shade as % sunlight 0-25%	26-50%	51-75%	76-100%	Reference
Coconut					
Brachiaria decumbens	0.7	4.4	9-11	28	Smith and Whiteman (1983)
Brachiaria humidicola	0.7	4.1	9-12	22	
Brachiaria miliiformis	1.0	3.4	4-7	18	
Stenotaphrum secundatum	1.9	4.9	3-4	6	
Axonopus compressus	1.3	1.9	4-5	5	
Paspalum conjugatum	1.0	2.6	2	8	
Ischaemum aristatum	.03	5.5	7-8	14	
Stylosanthes guianensis	-	-		15.2	Steel and Humphreys (1974)
Centrosema pubescens	-	-		3.3	
Panicum maximum (tall)			15.5		Reynolds (1978)
Brachiaria humidicola	-	-	10.5	-	
Brachiaria brizantha	-	-	8.9		
Brachiaria miliiformis		-	8.2	-	
Paspalum conjugatum	-	-	8.5		
Brachiaria brizantha			5-11	-	Manidool (1984)
Axonopus compressus	-	-	4-7	-	
Paspalum conjugatum			4-7	-	
Panicum maximum			1		
Rubber					
Brachiaria miliiformis	1.2	4.3	8.4	8.8	Waidyanatha et al. (1984)
Panicum maximum	2.2	6.1	8.9	11.1	
Brachiaria brizantha	2.1	5.6	8.6	10.1	
Panicum maximum	3.5	-	8.5	14.5	Mohd Najib (1989)
Pennisetum purpureum	4.2		9.5	12.3	
Oil Palm					
Panicum maximum	1.0		–		Chen and Bong (1983)
Axonopus compressus	.9	–	–	–	
Paspalum conjugatum	1.0	–	–	–	
Setaria sphacelata	0.6	–	–	–	
Digitaria setivalva	1.0	–	–	–	
Brachiaria decumbens	1.7	–	–	–	
Desmodium ovalifolium	2.0	–	–	–	Chen and Othman (1984)
Calopogonium caeruleum	0.6	–	–	–	
Centrosema pubescens	0.4	–	–		
Stylosanthes guianensis	0.3	–	–		
Desmodium heterophyllum	0.3	–			

[a] estimated

particularly *Panicum,* and *Brachiaria* and *Desmodium,* have the potential to improve forage supply.

The declining DM yield with decreasing light levels and the increased sensitivity of shaded grasses to defoliation necessitate proper management to ensure high productivity and persistence in a rapidly changing light environment. Persistent shade-tolerant species are needed for the long-term productivity and economic viability of integrated land-use systems.

Species that show high productivity and forage. quality in a wide range of light levels (90 to 20% of full sunlight) are desirable but are presently not available.

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Table 6. Persistence (expressed as % of initial plant density) of some tropical grasses as affected by defoliation frequency under the closed canopy of oil palm.

	Cutting interval (weeks)			Mean persistence
	8	12	16	
High shade tolerance				
Paspalum conjugatum	172	156	510	279
Axonopus compressus	594	557	323	491
Medium shade tolerance				
Panicum maximum	6	3	20	10
Digitaria setivalva	2	42	67	37
Brachiaria decumbens	4	44	56	35
Low shade tolerance				
Setaria sphacelata cv. Kazungula	5	7	1	4
Digitaria decumbens cv. Transvale	4	1	47	17

Source: Chen and Bong 1983.

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