

Growth responses of three *Brachiaria* species to light intensity and nitrogen supply

O. GUENNI¹, S. SEITER² AND R. FIGUEROA³

¹ Universidad Central de Venezuela (UCV),
Facultad de Agronomía, Instituto de Botánica
Agrícola, Maracay, Venezuela

² Department of Agricultural Sciences,
Linn-Benton Community College, Albany,
Oregon, USA

³ Universidad Central de Venezuela (UCV),
Facultad de Agronomía, Instituto de Ingeniería
Agrícola, Maracay, Venezuela

Abstract

Biomass production, dry matter partitioning and nutrient accumulation of 3 *Brachiaria* species (*B. brizantha*, *B. decumbens* and *B. dictyoneura*) were investigated under 3 photon flux densities (100, 57 and 29%) and 2 levels of soil N availability (with and without N added). Plants were grown in a controlled greenhouse under shade cloths in pots containing a mixture (1:1) of field soil and perlite. Measurements were carried out at the end of 2 growth periods: 34 days after planting (GP) and 41 days after cutting (RGP). Artificial shade reduced biomass production during both growth periods but the effect was greater during GP. Nitrogen availability played an increasing role only as the study progressed. A light intensity \times N interaction was observed in *B. brizantha* and *B. decumbens*, but not in *B. dictyoneura*. Shading increased plant allometric ratios and leaf N concentration. At 57% sunlight, total plant biomass in *B. brizantha* and *B. decumbens* was similar to that at full light conditions, when no N was added to the soil. *B. dictyoneura* had the lowest potential to adjust to restricted light conditions. The implications of these results in terms of forage yield and quality, and persistence under defoliation are discussed.

Introduction

Light availability is a major ecological factor influencing plant growth and survival. Plants can respond with genetic adaptation and phenotypic acclimation to low levels of irradiance (Lambers *et al.* 1998). Shade tolerance of species adapted to open habitats will depend on the capacity of the plants to adjust morphologically and physiologically to a given level of irradiance. Three major acclimation responses to shade have been observed: a) a reduction in the respiration rate, b) an increase in the shoot to root partitioning and c) an increase in the specific leaf area with a relatively low leaf mass ratio (Humphreys 1994; Lambers *et al.* 1998).

At the ecosystem level, reduced irradiance has a considerable impact on plant productivity. In water- and nutrient-limited environments, there is increasing evidence that substantial improvements in herbage yield and forage nutrient quality can be obtained when C₄ grasses are grown under tree shade in tropical and subtropical grasslands. A critical factor for better performance is the increased soil nutrient availability beneath the tree canopy (Wilson *et al.* 1990; Belsky 1992; Wilson 1996; Scholes and Archer 1997). According to Wilson (1996), the most consistent benefit from shade is better soil moisture, leading to a higher soil organic matter breakdown and, therefore, more available N in the soil. Surface litter and root turnover may also play a critical role, lowering the soil C:N ratio and, therefore, improving microbial activity and N cycling (Sánchez *et al.* 1997; Cruz *et al.* 1999).

Neotropical savannas cover very extensive areas in northern South America (Sarmiento 1990) and occupy almost a third of Venezuela (Huber 1987). The Orinoco Llanos, the largest continuous savanna ecosystem (Sarmiento 1990), is characterised by a sparse canopy of upright tillers (Sarmiento 1984). In some areas, leguminous trees are widespread and constitute the main food source for cattle during the dry season. Enhanced

Correspondence: Orlando Guenni, Instituto de Botánica Agrícola, Facultad de Agronomía, Universidad Central de Venezuela, Apartado Postal 4579, Maracay 2101, Venezuela. E-mail: guenni@agr.ucv.ve

cattle productivity in this ecosystem has been achieved by replacing native pasture species with perennial African forage grasses such as *Brachiaria* spp. and *Andropogon* spp. with higher forage quality and higher yields (CIAT 1982; Lascano 1991; Pizarro *et al.* 1998). The practice of clearing neotropical forests and savanna-forest ecotones for animal production is a controversial issue because of concerns about land degradation, loss of biodiversity and ecosystem sustainability (Maass 1995; Zimmer and Euclides-Filho 1997; Williams and Baruch 2000). It is therefore important to understand the performance of introduced species under restricted light conditions, as they represent the new companions for the woody component of the savanna.

Some *Brachiaria* species have been used as soil cover and forage in tropical tree plantations (Humphreys 1994; Stür *et al.* 1998) and have a high potential as energy banks when intercropped with shrub legumes such as *Leucaena leucocephala* and *Gliricidia sepium* in the wet and dry tropics (Gutteridge and Shelton 1994). Several studies have shown that *B. decumbens*, *B. brizantha* and *B. humidicola* perform well in medium shade (Humphreys 1994). Shelton *et al.* (1987) and Stür (1991) ranked them, together with *Panicum maximum*, as having medium shade tolerance. Both *B. decumbens* cv. Basilisk and *B. brizantha* CPI 15890 outyielded *B. humidicola* under a coconut canopy (Kaligis and Sumolang 1991; Rika *et al.* 1991), though Smith and Whiteman (1983) found no differences in shoot yield of *B. decumbens* and *B. humidicola* growing under similar conditions. Leaf elongation rate under shade was higher in *B. brizantha* cv. Marandu than in *B. humidicola*, suggesting a better tolerance of decreasing light conditions in the former species (Dias-Filho 2000).

The main objectives of this study were to: evaluate the responses of 3 *Brachiaria* species to different light intensities; and assess any potential interaction between incoming radiation and soil N on plant traits that might improve persistence under shade.

Materials and methods

The experiment was carried out in a controlled environment greenhouse with glass glazing at the University of New Hampshire, Durham (43°8'N, 70°56'W). Daily temperature was in the

range 24–36°C. Photoperiod varied from 13 to 14.5 hours.

Plant material

Three C₄ (subtype PEP-CK) African tropical grasses (Renvoize *et al.* 1998) with distinct growth habits were used: *B. brizantha* CIAT 6780 (a bunch plant), *B. dictyoneura* CIAT 6133 (mostly a prostrate and slow-growing plant which is considered morphologically similar to *B. humidicola*, Renvoize *et al.* 1998) and *B. decumbens* CIAT 606 (a semi-erect plant). Seeds were germinated in seedling trays containing peat moss. After 15–20 days of growth (2–3 leaves on the main stem), the grass seedlings were transplanted into plastic pots (25–29 cm diameter × 33 cm height) containing 10 kg of a dry mixture (1:1) of field soil and coarse perlite (The Scotts Company, Marysville, Ohio, USA). The chemical composition of the field soil was: pH — 5.2, total N — 3 g/kg, OM — 72 g/kg, estimated C:N ratio — 14.9, CEC — 2.4 mmol/kg, macronutrients (mg/kg) — 3.0, 131.3, 308.8 and 66.3 for P, K, Ca and Mg, respectively. After 4 days, plants were thinned to one per pot.

Experimental procedures

The experimental design was a factorial arrangement of 3 species × 3 light intensities × 2 N levels under a complete randomised design with 4 replicates.

The shade treatments were imposed 1 week after transplanting, when seedlings had developed at least 3 leaves. Light transmission into the greenhouse at noon was around 67 ± 2.1% of incident sunlight. Three regimes of photon flux density (PFD) at pot height were established by using artificial shade cloth placed 1.5 m above the pots. The shade cloths were mounted on metal frames (4 × 1.2 m) lying over a bench 0.9 m above ground and had about 1.0 m overhang to prevent access of direct sunlight to plants. Integrals of daily incident radiation at pot height resulted in the following PFD regimes (Figure 1): high (H) = 100% transmitted sunlight, medium (M) = 57% and low (L) = 29%. The spectral composition of the transmitted light was not measured. Generally, however, there is a slight increase of diffuse radiation in shaded treatments when shade cloth is used (Healey and Rickert 1998).

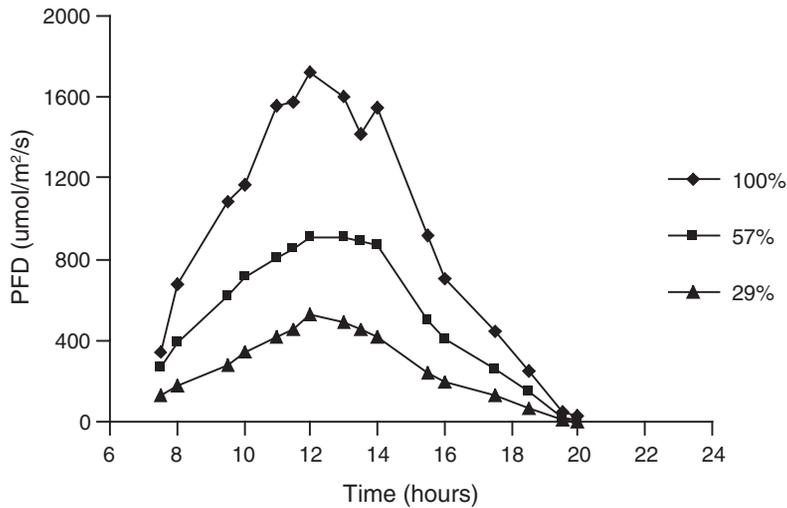


Figure 1. Diurnal patterns of photon flux density (PFD) for the different levels of light intensity (100, 57 and 29%) during the experiment.

The 3 grasses were grown under 2 nitrogen (N) levels: without N (–N) and with N (+N) added regularly as urea to the irrigation water. The +N treatments received 94 mg/pot of N 14 days after transplanting, and a further 2 doses of 188 mg/pot of N at days 35 and 63, giving a total of 470 mg/pot of N, equivalent to 70 kg/ha. The only N source for the plants growing in the –N pots was soil N. At the beginning (Day 10) and the middle of the experiment (Day 39), all pots were supplemented with a fertiliser solution containing the following nutrients (mg/pot): P (213), K (617), Ca (700), Mg (134) and S (185).

During the experiment, irrigation was applied as necessary to maintain soil near field capacity. Soil matrix potential was monitored by using tensiometers randomly installed in 4 pots within each shade treatment.

Harvesting and measuring of plants

Two harvests divided the experiment into 2 growth periods, the first of which (GP) lasted 34 days from transplanting (or 27 days after the shade cloth was erected over the plants). At the end of the GP, plants were cut at 5 cm above ground. The harvested material was separated into green leaf-blades, stems and dead biomass. All plants were left to regrow for 41 days (RGP). At the end of the RGP, all plant parts were harvested and separated into tillers (*i.e.*, green

leaf-blades + stems), roots, dead material, inflorescences and crown-stubble component (2–3 cm above and 1–2 cm below soil surface).

At each harvest, a green leaf-blade sample was randomly selected to measure specific leaf area (SLA), leaf area per plant (LA) and the LA:total plant dry weight ratio (LAR) using a leaf area meter (LICOR 3200, LICOR Inc., USA). Another leaf sample was dried and ground to determine the concentration of total N (Kjeldahl digestion), P (molybdenum-blue method) and K (spectrophotometric atomic absorption technique).

The numbers of leaves and tillers (*i.e.*, numbers of both fully expanded leaf-blades and stems per plant per week) were recorded in each pot during GP and RGP.

Measurements of plant environment

PFD and air temperature measurements were recorded several times during the experiment on 3 consecutive clear days by using a linear quantum sensor (Ceptometer SF-80, Decagon Devices, Inc., Pullman, WA, USA) and standard maximum-minimum air thermometers. Soil temperature at 2–3 cm depth was continuously recorded with sensors (HOBO® temperature logger, Onset Computer Corporation, MA, USA), which were randomly located in 4 pots per shade treatment. In addition, soil temperature at 5–7 cm depth was also recorded in the same pots at the

time PFD and air temperature were monitored. For this purpose, 4 soil thermometers were used in each shade treatment.

Data analysis

Means of the measured variables were compared by using the appropriate ANOVA procedure (SAS Institute 1989) and the Duncan test ($P < 0.05$). Plant variables were normalised accordingly by using the appropriate numeric transformation (Zar 1984).

Results

Light conditions, air and soil temperature under shade

Maximum incident and transmitted PFD on a typical day during the experiment occurred at around 12.00–14.00 h, and decreased from 1542 $\mu\text{mol}/\text{m}^2/\text{s}$ (H regime) to 869 and 420 $\mu\text{mol}/\text{m}^2/\text{s}$ for the M and L regimes, respectively (Figure 1).

Until midday, air temperature was slightly higher in the full light treatment, but differences between light intensities declined as the afternoon advanced. Peak air temperatures were recorded at noon, varying from 32°C (M and L) to 36°C (H). Maximum soil temperatures were recorded between 12.00 h and 14.00 h, and at 13.00 h varied from 26°C (L) to 30°C (H) at 2.5 cm, with a range of 24–29°C for the same treatments at 5.5 cm depth.

Yield components after first growth period

Flowering occurred during both experimental periods (GP and RGP), but only in *B. decumbens* and *B. dictyoneura*. Reproductive structures and dead tissue represented a very small fraction of total plant dry weight, with maximum values of 4% and 7%, respectively, at the second harvest (RGP).

At the end of the first growth period (GP), light intensity was the overriding environmental factor affecting the growth response of the 3 grasses, followed by species and N level. Shade decreased ($P < 0.05$) final shoot biomass and its components in all species and at both N levels (Table 1), with

Table 1. Dry weight (g/plant) of shoots, green leaves and stems, number of leaves and tillers, total leaf area (LA, dm^2/plant) and specific leaf area (SLA, cm^2/g) of three *Brachiaria* species at the end of the growth period (GP) under different light intensities and N levels.

Species, N level ¹	Light Intensity ²	Shoot	Green leaf	Stem	Leaf number	Tiller number	LA	SLA
<i>B. brizantha</i>								
+N	H	26.9a ³	18.1a	8.8a	73.3a	27.0a	43.1a	240.3c
	M	18.1b	11.0b	7.0a	48.8b	17.0b	34.5b	314.5b
	L	5.9c	3.6c	2.3b	23.3c	10.0c	14.1c	389.2a
-N	H	16.4a	11.3a	5.2a	70.0a	23.0a	26.0a	231.3c
	M	10.3b	6.6b	3.7b	36.5b	14.8b	20.6a	313.9b
	L	3.8c	2.5c	1.2c	18.0c	8.0c	9.4b	375.9a
<i>B. decumbens</i>								
+N	H	32.8a	14.7a	17.8a	160.5a	60.8a	39.2a	265.0c
	M	22.5b	9.4b	12.8b	104.8b	41.3b	33.7a	357.0b
	L	7.4c	3.8c	3.6c	46.0c	19.0c	18.1b	471.8a
-N	H	26.6a	10.9a	15.4a	153.0a	51.8a	26.0a	239.6c
	M	14.2b	6.5b	7.6b	78.3b	31.3b	21.5b	331.2b
	L	5.5c	2.7c	2.7c	38.0c	14.3c	11.5c	419.9a
<i>B. dictyoneura</i>								
+N	H	15.8a	6.0a	9.8a	153.3a	48.8a	14.2a	234.5b
	M	8.3b	4.2b	4.2b	51.8b	22.5b	11.6a	282.2a
	L	2.1c	1.3c	0.8c	16.5c	9.3c	4.2c	314.2a
-N	H	11.4a	4.1a	7.2a	109.0a	30.8a	10.2a	245.0b
	M	5.6b	2.9b	2.7b	37.8b	20.5b	7.4b	254.0b
	L	1.8c	1.2c	0.6c	16.3c	9.5c	3.6c	305.3a

¹ +N: with N fertilisation; -N: without N fertilisation.

² H: 100% light; M: 59% light; and L: 29% light.

³ For each species, values within columns and N levels followed by different letters are different ($P < 0.05$).

the largest depression in shoot yield (77–87% for all species and soil N conditions) at the low light regime (L). The corresponding ranges were 71–79% and 74–92% for leaf and stem biomass, respectively. The reduction in aerial biomass was almost proportional to the reduction of irradiance. Responses in shoot yield to N application were 35–64%, while the highest-yielding species (*B. decumbens*) produced 2.4 times as much shoot DM as the lowest (*B. dictyoneura*). As a result of the reduction in stem dry weight, the leaf-blade:stem ratio in *B. dictyoneura* was significantly increased ($P < 0.05$) from 0.6:1 in full light conditions (H) to 1.8:1 at low light intensity (L). This ratio was relatively less affected in *B. brizantha* (1.7:1 to 2.1:1) and *B. decumbens* (0.8:1 to 1.0:1) (data not shown).

Leaf area per plant (LA) varied with species and was affected by light intensity and soil N condition. *B. brizantha* and *B. decumbens* had higher LA than *B. dictyoneura*. Across species and N levels, leaf area was reduced by 54–71% under low light intensity compared with full light conditions (Table 1). Specific leaf area (SLA) increased ($P < 0.05$) in each species with decreasing light intensity, as a result of greater reductions in leaf biomass than in LA. Decreased leaf biomass and number with shade was in turn the result of a lower number of tillers producing leaves (Table 1), as the number of leaves per tiller remained relatively constant over species and N levels (data not shown).

There was a general trend for N, P and K (data not shown) concentrations in leaf tissues to increase with decreasing light intensity. For *B. decumbens*, P concentration increased significantly ($P < 0.05$) as light intensity declined from H to L at both N levels, increasing from 27 g/kg to 32 g/kg and from 21 g/kg to 32 g/kg for –N and +N treatments, respectively. The increase in leaf K from H to L was also significant ($P < 0.05$) in all cases, with a maximum range of 40–61 g/kg for *B. decumbens* at –N. The increase in leaf N with shading was lower than the increase in K, and was significant ($P < 0.05$) for *B. brizantha* and *B. decumbens* at both soil N levels, with a maximum variation of 30–38 g/kg (*B. decumbens* at –N).

Yield components after second growth period

By the time of the second harvest (end of RGP), all factors (light, N level and species) had significant effects on growth. However, the effects of

light intensity on biomass production and allocation were more dependent on soil N conditions, because interactions between light intensity and soil N level were also highly significant ($P < 0.0001$) for most plant components considered.

In all +N treatments, plant biomass and tiller number (data not shown) of all species decreased with decreasing available light (Figure 2). However, green leaf and stem biomass were generally not reduced ($P > 0.05$) at the medium light intensity. Without supplemental N, shoot and stem yields of *B. brizantha* and *B. decumbens* were significantly ($P < 0.05$) higher at M than at H and L light intensities, while for *B. dictyoneura* H and M regimes produced more biomass than L (Table 2). For all species, leaf production was higher at H and M than at L light intensity. Final numbers of leaves and tillers were significantly reduced ($P < 0.05$) only at the L regime in all species (data not shown).

At +N, a larger but not statistically significant LA was observed in the medium light intensity treatment in all species (Figure 3). At –N, shade had no significant effect on LA in *B. dictyoneura*, but resulted in higher LA in the other species. Higher LA values at the M regime were the net result of leaf biomass comparable with that produced under the H regime (Table 2) and higher values of SLA in all species when grown under shade (Figure 4). In this case, leaf area per unit leaf mass increased with decreasing light intensity. The increase in SLA was generally accompanied by leaf blades being longer and narrower than when grown in full light. This was particularly the case in *B. dictyoneura*.

Under both N levels, restricted light resulted in a sharp decrease ($P < 0.05$) in crown biomass (Table 2). The reduction from H to L was 84–86, 88–94 and 91–93% for *B. decumbens*, *B. brizantha* and *B. dictyoneura*, respectively. Root dry weight was also highly affected by shade, with a reduction of 91–97% over species and N levels. Very little root biomass was observed in *B. dictyoneura* at the L light regime (0.15 ± 0.07 g/plant).

The higher reduction in below-ground biomass in comparison with above-ground biomass with decreasing light intensity resulted in a dramatic change in biomass partitioning between shoots and roots. The shoot:root (S:R) ratio was 6–17 times higher at low light than full light (Table 2), with higher differences on the –N treatments. As leaf biomass was promoted at the expense of root

and crown biomass, and because of the proportional increase in SLA with shade, LAR (leaf area per plant:total plant dry weight ratio) increased from H to L in all species (Table 2).

During RGP, N supply and light intensity affected leaf N concentration more strongly than species, with a significant light intensity \times soil N interaction ($P < 0.0001$). Final leaf N concentration was generally higher at +N (Figure 5). Plants grown under low N supply and high irradiance had visual symptoms of chlorosis and a higher proportion of dead material (data not shown). However, within soil N levels, N concentration in leaves increased significantly ($P < 0.05$) with shading, particularly in *B. brizantha* and *B. decumbens*. For instance, at low soil N, the amount of leaf N increased with shading from

8.7 g/kg to 29.1 g/kg, 11.7 g/kg to 32.2 g/kg and 13.8 g/kg to 26 g/kg in *B. brizantha*, *B. decumbens* and *B. dictyoneura*, respectively.

When calculated on a leaf area basis, the leaf N content or specific leaf nitrogen (SLN, g/m²) showed only a slight increase with decreasing light intensity. This was particularly the case under -N conditions, where SLN increased with shade from 0.5 g/m² to 0.8 g/m² and from 0.6 g/m² to 0.8 g/m² for *B. brizantha* and *B. decumbens*, respectively. For +N, values of SLN tended to decrease (*B. decumbens* and *B. dictyoneura*) or remain steady (*B. brizantha*) with decreasing light intensity.

By the end of the RGP, K concentration in leaf tissue followed the same trend with shade as that observed with leaf N. In all species, the

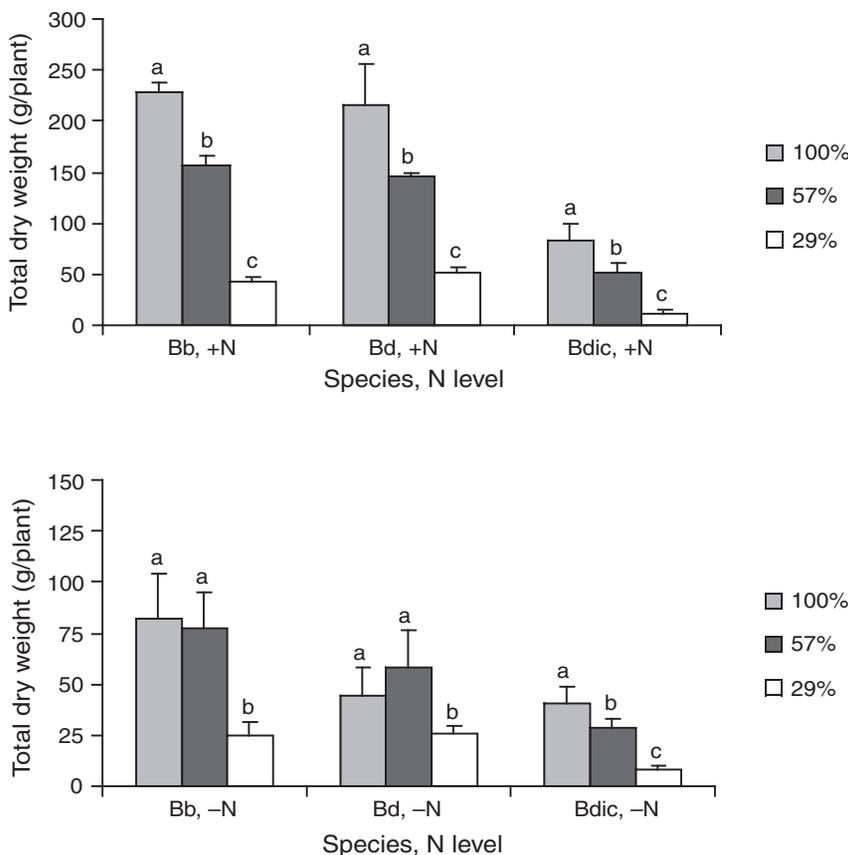


Figure 2. Total plant biomass per pot at the end of the regrowth period (RGP), under different light intensities (100, 57 and 29%) and soil N availabilities (+N with N fertilisation; -N without N fertilisation). Bb: *B. brizantha*, Bd: *B. decumbens* and Bdic: *B. dictyoneura*. Vertical lines refer to the SD ($n = 4$) of each mean value. Different letters within species and N levels mean significant differences ($P < 0.05$) among light intensities.

Table 2. Final dry weight (g/plant) of shoots, green leaves, stems, crown and roots, shoot:root (S:R) ratio and leaf area ratio (LAR, dm²/g of plant dry weight) of three *Brachiaria* species at the end of the regrowth period (RGP) under different light intensities. H: 100% light, M: 59% light and L: 29% light. +N: With N fertilisation, -N: Without N fertilisation. For each species, different letters within the same column and N level mean significant differences (P<0.05) among light intensities.

Species, N level	Light intensity	Shoot	Green leaf	Stem	Crown	Roots	S:R	LAR
<i>B. brizantha</i>								
+N	H	136.2a	61.9a	66.8a	55.6a	37.0a	3.8c	0.6c
	M	118.8b	58.2a	59.3a	21.0b	15.8b	7.6b	1.0b
	L	37.4c	19.5b	17.8b	3.6c	1.7c	22.3a	1.6a
-N	H	35.5b	17.7a	15b	18.2a	28.2a	1.2c	0.4c
	M	58.2a	25.5a	30.8a	8.9b	9.8b	6.1b	0.9b
	L	21.4c	10.6b	10.3b	2.1c	1.1c	20.2a	1.6a
<i>B. decumbens</i>								
+N	H	146.0a	39.6a	89.1a	25.6a	42.9a	3.7c	0.4c
	M	120.3b	35.3a	74.8a	11.6b	13.1b	9.3b	0.9b
	L	45.8c	17.3b	25.8b	3.6c	2.1c	22.0a	1.5a
-N	H	24.2b	6.7a	13.5b	7.4a	12.8a	1.9c	0.3c
	M	43.7a	11.4a	28.2a	5.3b	8.9b	4.9b	0.6b
	L	23.3b	8.0a	13.8b	1.2c	1.2c	19.6a	1.3a
<i>B. dictyoneura</i>								
+N	H	68.4a	16.6a	44.2a	8.6a	5.0a	15.5b	0.4c
	M	44.8b	13.5a	27.3b	5.0b	1.9b	23.5b	0.8b
	L	10.2c	4.5b	5.5c	0.6c	0.1c	101.0a	1.4a
-N	H	28.0a	5.9a	19.2a	5.0a	7.4a	4.0c	0.3c
	M	24.0a	6.3a	14.0a	2.4b	2.2b	11.0b	0.6b
	L	7.9b	3.3b	4.3b	0.4c	0.2c	42.7a	1.2a

concentration of K was consistently higher (P<0.05) under the M and L regimens. Across the two soil N conditions, leaf K increased with shade from 30 ± 1 g/kg to 54 ± 1 g/kg, 24 ± 1 g/kg to 46 g/kg, and 36 ± 3 g/kg to 52 ± 3 g/kg for *B. brizantha*, *B. decumbens* and *B. dictyoneura*, respectively. Leaf P was much less influenced by light intensity and soil N, with a maximum range of variation from 1.8 ± 0.1 g/kg (H) to 4.1 ± 1.8 g/kg (L) over the 3 species and soil N levels.

Discussion

This study has provided interesting information on the effect of shading on 3 widely used commercial grass species, which could be used in silvopastoral systems.

Effects on biomass production and carbon allocation

The superior growth of *B. brizantha* and *B. decumbens* relative to *B. dictyoneura*, through higher shoot and crown biomass and more developed root systems, supports the similar

differences in biomass production observed between *B. brizantha* and *B. humidicola* (Dias-Filho 2000) under greenhouse conditions. The dramatic impact of shade in reducing dry matter yield, especially during the first 34 days of growth (GP), again reinforced similar reports in the literature (Norton *et al.* 1991; Cruz 1997b; Cruz *et al.* 1999; Durr and Rangel 2000).

As nutrient demand increased during RGP, interactions between N availability and plant response to light emerged. While light intensity remained the primary limiting factor for growth at high N levels, there was a different situation at low N levels. At the low N level, light was the primary limiting factor until the medium light intensity was reached. However, plants could not respond to the highest light intensity at this limited level of N. This effect was more evident in *B. brizantha* and *B. decumbens* than in *B. dictyoneura*.

Durr and Rangel (2000) found no shade effects on forage yield of *Panicum maximum* when grown in pots with low soil fertility. They attributed this lack of response to artificial shade to a severe limitation of photosynthetic activity and, consequently, biomass accumulation caused by insufficient soil N and P. In our experiment, in the absence of additional N, the positive growth

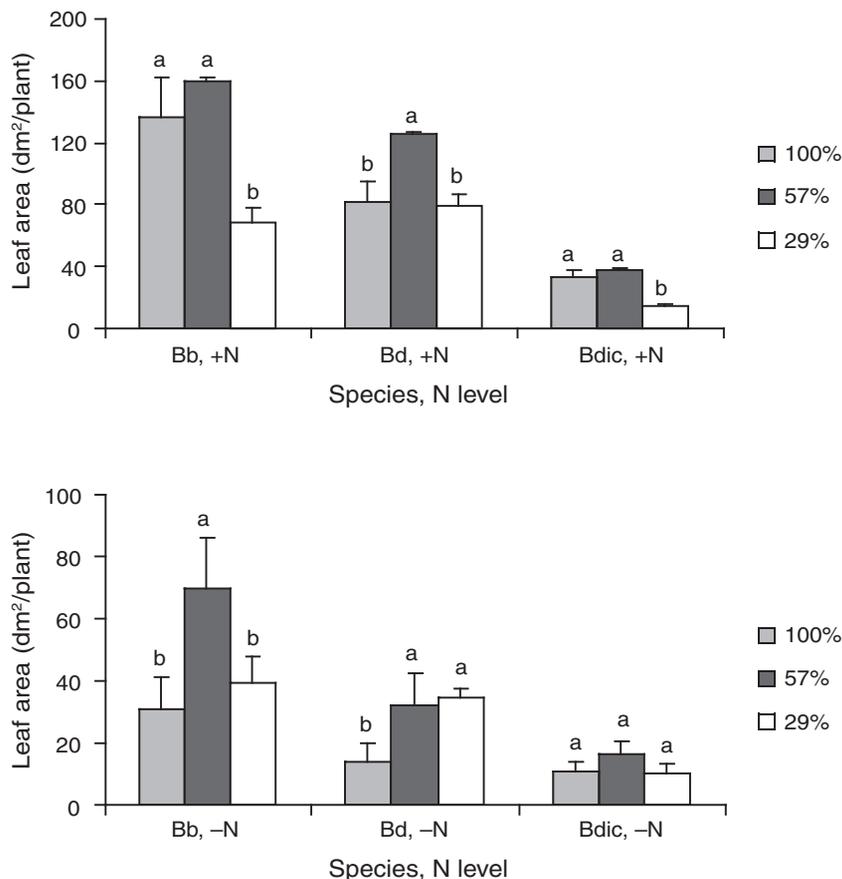


Figure 3. Leaf area per plant (LA) at the end of the regrowth period (RGP), under different light intensities (100, 57 and 29%) and soil N availabilities (+N with N fertilisation; -N without N fertilisation). Bb: *B. brizantha*, Bd: *B. decumbens* and Bdic: *B. dictyoneura*. Vertical lines refer to the SD ($n = 4$) of each mean value. Different letters within species and N levels mean significant differences ($P < 0.05$) among light intensities.

responses to increases in light intensity from L to M indicated that the inherent nutrient content of the soil was enough to promote significant growth, with light intensity being the primary limiting factor. Eriksen and Whitney (1981) also observed a marked increase in plant growth without supplemental N in *P. maximun*, *B. miliformes* and to a lesser degree *B. brizantha* over a wide range of fractional daylight (*i.e.*, 100–45%). These results support other observations (Wilson *et al.* 1986; Samarakoon *et al.* 1990; Cruz *et al.* 1999) that such positive responses to limited light conditions are restricted not only to grasses growing in the understory of leguminous or non-leguminous tress (Wilson *et al.* 1990; Cruz 1997a), but also to those growing under artificial shade. However,

when soil water and nutrients are not limiting, a reduction in grass biomass under severe light restriction is expected when compared with full light conditions (Cruz *et al.* 1999).

The observed beneficial effects of artificial shading on forage yield and nutrient concentrations in *B. decumbens*, *B. brizantha* and other C_4 grasses may be explained by Wilson's hypothesis (1990), which relates positive growth responses in pastures to a better availability of soil N. This is supported by the enhanced leaf N concentration at similar plant biomass for the -N treatment, which in turn seemed to be explained by improved conditions for soil N mineralisation. A decrease in midday temperature (2–3°C) at 57% radiation compared with full light may have created more

favourable conditions for soil microbial activity and nutrient uptake in these species grown in pots (Wilson and Wild 1995).

Common effects of shade on resource allocation include an increase in the leaf proportion and SLA, and a decrease in dry matter content, which maximise light interception with minimum energy investment (Cruz *et al.* 1999; Durr and Rangel 2000). The 3 *Brachiaria* species used in this study displayed morphological plasticity to improve light interception in response to low irradiance, expressing it primarily by a dramatic increase in the carbon allocation to the above-ground biomass.

The magnitude of the increases in shoot:root ratio in response to shade (6.5–10.7 times higher in low light regimens than in full light)

contrasts with the finding of Wong *et al.* (1985), who reported only a 2.8-fold increase in 12 tropical and subtropical grasses (including *B. decumbens* and *B. brizantha*) grown at a similar range of light intensities. Similarly, Durr and Rangel (2000) showed an increase in the shoot:root ratio of 3.4 times when *P. maximum* was exposed to 12% of total sunlight, while Ludlow *et al.* (1974) also found a common increase in this plant trait in forage legumes.

At early vegetative growth, total leaf area at intermediate light intensities was often not affected, because increase in leaf area per unit of mass compensated for reduced leaf weight and leaf number per plant. This increment in SLA was evident even when other plant components like crown and roots were actively competing for photosynthates.

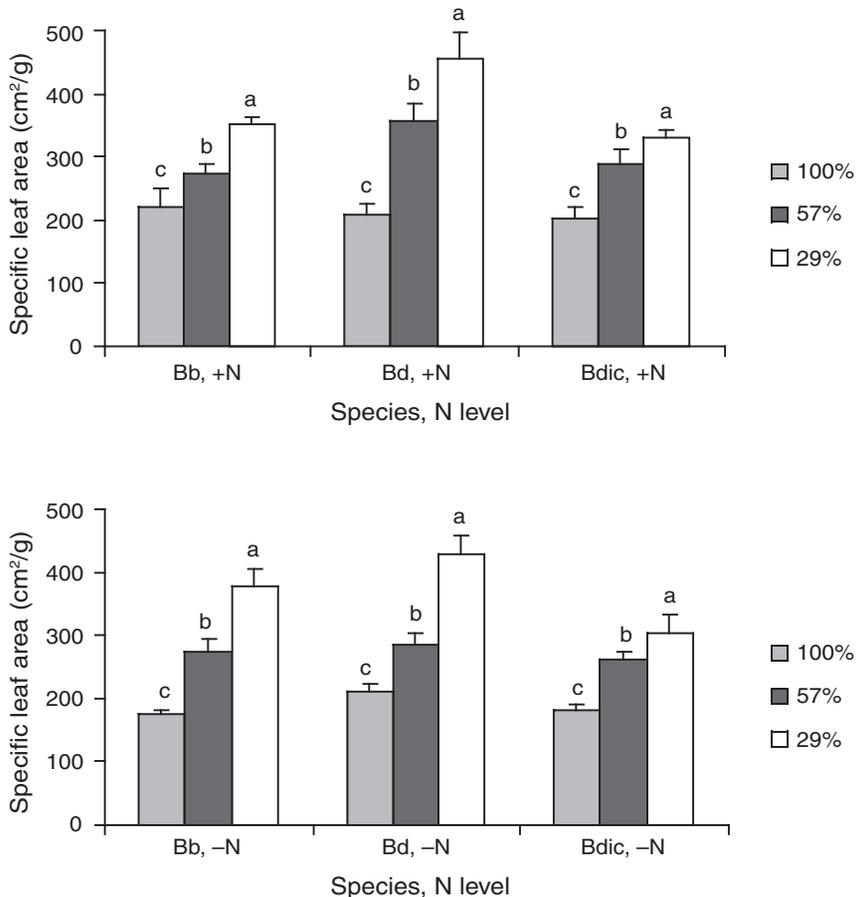


Figure 4. Specific leaf area (SLA) at the end of the regrowth period (RGP), under different light intensities (100, 57 and 29%) and soil N availabilities (+N with N fertilisation; -N without N fertilisation). Bb: *B. brizantha*, Bd: *B. decumbens* and Bdic: *B. dictyoneura*. Vertical lines refer to the SD (n = 4) of each mean value. Different letters within species and N levels mean significant differences (P < 0.05) among light intensities.

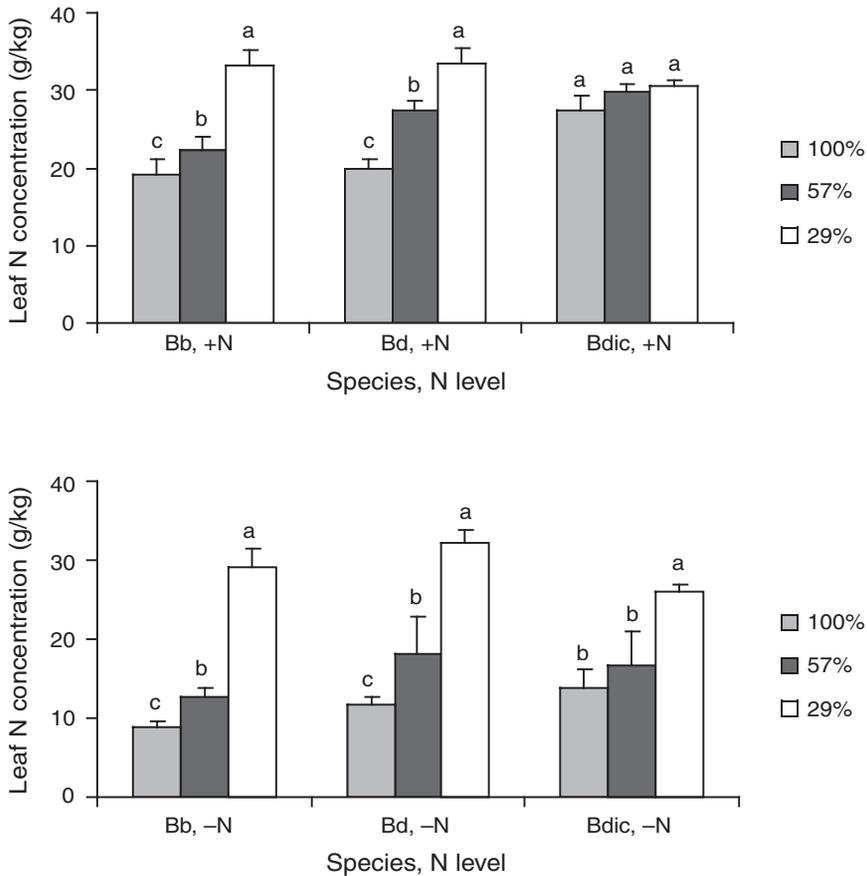


Figure 5. Leaf N concentration at the end of the regrowth period (RGP), under different light intensities (100, 57 and 29%) and soil N availabilities (+N with N fertilisation; -N without N fertilisation). Bb: *B. brizantha*, Bd: *B. decumbens* and Bdic: *B. dictyoneura*. Vertical lines refer to the SD ($n = 4$) of each mean value. Different letters within species and N levels mean significant differences ($P < 0.05$) among light intensities.

However, after regrowth, biomass allocation to leaves was significantly affected at the lowest light intensity. Previous acclimation to shade appeared to result in a large increase in LA:total plant dry weight ratio (LAR) (Kephart *et al.* 1992) after regrowth, which was in turn greatly stimulated by an increase in SLA and total leaf area at all N conditions. The increase in LAR with shade has been positively associated with better nutritive value in forage grasses (Kephart and Buxton 1993).

Effect on leaf nutrients

The observed increase in the N concentration of leaves of the *Brachiaria* species in response to shade is consistent with the results found in other

C_4 and C_3 grasses (Wilson *et al.* 1990; Wilson and Wild 1991; Norton *et al.* 1991; Kephart and Buxton 1993; Deinum *et al.* 1996; Durr and Rangel 2000). In addition, the increase in leaf-N concentration in the *Brachiaria* species under shade was not always associated with lower plant yield, as may be expected particularly when soil N is high (Cruz *et al.* 1995). Thus, continued accumulation of N in the plant seems to be regulated by C assimilation and partitioning, unless a differential N allocation between shoot and roots (not measured in this study) may have occurred under shade. Cruz (1997b) found that, under 56% sunlight, nitrogen was preferentially allocated to green leaves at the expense of allocation to other plant components in *Dichanthium aristatum*.

The observed increases in leaf N, P and K across grass species at restricted light intensities also support Wilson's hypothesis (1990) that, under natural conditions, shade leads to a greater soil organic matter breakdown and N turnover. Cruz (1996; 1997a) found that N uptake by shaded stands of *D. aristatum* in the field was always higher than by stands receiving full sunlight for any given level of aerial biomass. This and a higher shoot:root ratio allowed shaded leaves with higher N concentrations to improve their photosynthetic light response, resulting in higher radiation use efficiency (RUE) in unfertilised shaded stands.

Cruz (1997b) argued that the improvement of SLN of shaded leaves was a mechanism that compensated for limited light availability. Although the increase in this plant trait with shade was not significant in our study, the SLN values were close to the theoretical values of 1–1.2 g/m², which correspond with maximum RUE for a C₄ plant (Sinclair and Horie 1989). Under field conditions where N availability is limiting, a higher SLN could increase C assimilation and consequently RUE of shaded pastures (Sinclair and Horie 1989; Wilson and Ludlow 1991; Cruz *et al.* 1995; Cruz 1997a). The potential improvement of RUE under shade in these *Brachiaria* species may be associated with a higher photosynthetic activity and a lower dark respiration observed at low irradiance (Dias-Filho 2002).

Implications for pasture persistence under defoliation

An increase in C allocation to above-ground biomass at the expense of crown and root biomass is a common response in forage plants to maximise light capture under restricted irradiation conditions (Samarakoon *et al.* 1990; Wilson *et al.* 1990; Wong 1991; Paez *et al.* 1994; Cruz 1997b). The level of this response has important implications for plant survival. A marked reduction in crown biomass and the excessive increase in the shoot:root ratio with shade, as reported in this study, may threaten long-term persistence of these perennial forage grasses because the lack of sufficient rooting and poor buildup of reserves could compromise survival under grazing (Wilson and Ludlow 1991; Wong and Stür 1996; Dias-Filho 2000).

Consequently, it has been proposed that under shading, prostrate grasses may be better suited

for grazing or cutting than caespitose grasses, as the former are able to accumulate more residual foliage and growing buds after defoliation (Humphreys 1991; Wilson and Ludlow 1991; Wong and Stür 1996). However, the significant reduction in plant growth and biomass allocation to roots reported here for the stoloniferous *B. dictyoneura* and a similar grass, *B. humidicola* (Dias-Filho 2000), when grown under reduced light, does not seem to support this hypothesis. Differential accumulation of residual leaf area and reserves at tiller bases, stolons and underground organs among species, may play a key role in the degree to which various pastures tolerate defoliation when grown in shade (Wilson and Ludlow 1991; Wong and Stür 1996). More detailed studies are required before management strategies for grazing are developed in selected species with relatively good persistence under shade.

Conclusions

This study supports the increasing body of evidence that, under certain conditions, shade as a single factor can improve shoot growth in C₄ perennial grasses commonly used as forage plants in the tropics. This beneficial effect seems to be associated with a higher nutrient availability, which is particularly important in nitrogen-deficient soils, such as those occurring in neotropical savannas.

Of the 3 *Brachiaria* species studied, *B. dictyoneura* appeared to have the lowest capacity to adjust to shade conditions (<50% of PFD), being unable to produce adequate leaf area and root biomass, while *B. brizantha* and *B. decumbens* showed a better tolerance of shade. However, it is well to remember that this was a glasshouse study with plants to 11 weeks of age. Moisture was not limiting and there were no trees competing with the plants for moisture and nutrients. More studies in the field are needed to confirm that these preliminary results can be reproduced under grazing in silvopastoral systems before recommendations can be made on their commercial use in these situations.

Acknowledgements

This study was undertaken when the first author was on research leave at the University of New Hampshire (UNH). Financial support was partially

provided by the Council of Scientific and Humanistic Development (CDCH) of the Universidad Central de Venezuela (UCV). Technical assistance provided by the personnel of the glasshouses complex of the UNH Plant Biology Department was greatly appreciated. Nutrient concentrations in plant samples were determined at the Animal Nutrition Laboratory of the Agronomy Faculty, UCV.

References

- BELSKY, A.J. (1992) Effects of trees on nutritional quality of understory gramineous forage in tropical savannas. *Tropical Grasslands*, **26**, 12–20.
- CIAT (Centro Internacional de Agricultura Tropical) (1982) *Informe CIAT 1982*. CIAT, Cali, Colombia.
- CRUZ, P. (1996) Growth and nitrogen nutrition of a *Dichanthium aristatum* pasture under shading. *Tropical Grasslands*, **30**, 407–413.
- CRUZ, P. (1997a) Effect of shade on the growth and mineral nutrition of a C_4 perennial grass under field conditions. *Plant and Soil*, **188**, 227–237.
- CRUZ, P. (1997b) Effect of shade on the carbon and nitrogen allocation in a perennial tropical grass, *Dichanthium aristatum*. *Journal of Experimental Botany*, **48(306)**, 15–24.
- CRUZ, P., TOURNEBIZE, C., GAUDICHAU, C., HAEGELIN, A. and MUNIER-JOLAIN, N.M. (1995) Effect of shade on growth, nitrogen content and CO_2 leaf assimilation in a tropical perennial grass. In: Sinoquet, H. and Cruz, P. (eds) *Ecophysiology of tropical intercropping*. pp. 284–293. (INRA: Paris).
- CRUZ, P., SIERRA, J., WILSON, J.R., DULORMNE, M. and TOURNEBIZE, R. (1999) Effects of shade on the growth and mineral nutrition of tropical grasses in silvopastoral systems. *Annals of Arid Zone*, **38(3&4)**, 335–361.
- DEINUM, B., SULASTRI, R.D., ZEINAB, M.H.J. and MAASSEN, A. (1996) Effects of light intensity on growth, anatomy and forage quality of two tropical grasses (*Brachiaria brizantha* and *Panicum maximum* var. *trichoglume*). *Netherlands Journal of Agricultural Sciences*, **44**, 111–124.
- DIAS-FILHO, M.B. (2000) Growth and biomass allocation of the C_4 grasses *Brachiaria brizantha* and *Brachiaria humidicola* under shade. *Pesquisa Agropecuária Brasileira*, Brasília, **35(12)**, 2335–2341.
- DIAS-FILHO, M.B. (2002) Photosynthetic light response of the C_4 grasses *Brachiaria brizantha* and *B. humidicola* under shade. *Scientia Agricola*, **59(1)**, 65–68.
- DURR, P.A. and RANGEL, J. (2000) The response of *Panicum maximum* to a simulated subcanopy environment I. Soil × shade interaction. *Tropical Grasslands*, **34**, 110–117.
- ERIKSEN, F.I. and WHITNEY, A.S. (1981) Effects of light intensity on growth of some tropical forage species. I. Interaction of light intensity and N fertilization on six forage grasses. *Agronomy Journal*, **73**, 427–433.
- GUTTERIDGE, R.C. and SHELTON, H.M. (1994) *Forage Tree Legumes in Tropical Agriculture*. (CAB International: Wallingford).
- HEALEY, K.D. and RICKERT, K.G. (1998) Shading material changes the proportion of diffuse radiation in transmitted radiation. *Australian Journal of Experimental Agriculture*, **38**, 95–100.
- HUBER, O. (1987) Neotropical savannas: their flora and vegetation. *Trends in Ecology and Evolution*, **2**, 67–71.
- HUMPHREYS, L.R. (1991) *Tropical Pasture Utilisation*. (Cambridge University Press: Cambridge).
- HUMPHREYS, L.R. (1994) *Tropical Pastures: Their Role in Sustainable Agriculture*. (Longman Scientific and Technical/John Wiley and Sons, Inc.: New York).
- KALIGIS, D.A. and SUMOLANG, C. (1991) Forages species for coconut plantations in North Sulawesi. *ACIAR Proceedings No. 32, Forages for Plantations Crops, Bali, 1990*. pp. 45–48.
- KEPHART, K.D., BUXTON, D.R. and TAYLOR, S.E. (1992) Growth of C_3 and C_4 perennial grasses under reduced irradiance. *Crop Science*, **32**, 1033–1038.
- KEPHART, K.D. and BUXTON, D.R. (1993) Forage quality responses of C_3 and C_4 grasses to shade. *Crop Science*, **33**, 831–837.
- LAMBERS, H., CHAPIN, F.S. III and PONS, T.L. (1998) *Plant Physiological Ecology*. (Springer-Verlag: New York).
- LASCANO, C.E. (1991) Managing the grazing resource for animal production in savannas of tropical America. *Tropical Grasslands*, **25**, 66–72.
- LUDLOW, M.M., WILSON, G.L. and HESLEHURST, M.R. (1974) Studies on the productivity of tropical pasture plants. V. Effect of shading on growth, photosynthesis and respiration in two grasses and two legumes. *Australian Journal of Agricultural Research*, **25**, 425–433.
- MAASS, J.M. (1995) Conversion of tropical dry forests to pastures and agriculture. In: Bullock, S.H., Mooney, H.A. and Medina, E. (eds) *Seasonally Dry Tropical Forests*. pp. 399–416. (Cambridge University Press: Cambridge).
- NORTON, B.W., WILSON, J.R., SHELTON, H.M. and HILL, K.D. (1991) The effect of shade on forage quality. *ACIAR Proceedings No. 32, Forages for Plantations Crops, Bali, 1990*. pp. 83–88.
- PAEZ, A., GONZÁLEZ, M.E. and PEREIRA, N. (1994) Comportamiento de *Panicum maximum* em condiciones de sombreado y de luz solar total. Efecto de la intensidad de corte. *Revista de la Facultad de Agronomía (LUZ)*, **11**, 25–42.
- PIZARRO, E.A., DO VALLE, C.B., KELLER-GREIN, G., SCHULTZE-KRAFT, R. and ZIMMER, A.H. (1998) Experiencia regional con *Brachiaria*: Región de América Tropical — Sabanas. In: Miles, J.W., Maass, B.L. and do Valle, C.B. (eds) *Brachiaria: Biología, Agronomía y Mejoramiento*. pp. 247–269. (CIAT, EMBRAPA/CNPQC: Cali).
- RENOUVE, S.A., CLAYTON, W.D. and KABUYE, C.H.S. (1998). Morfología, Taxonomía y Distribución Natural de *Brachiaria* (Trin.) Griseb. In: Miles, J.W., Maass, B.L. and do Valle, C.B. (eds) *Brachiaria: Biología, Agronomía y Mejoramiento*. pp. 1–17. (CIAT, EMBRAPA/CNPQC: Cali).
- RIKA, I.K., MENDRA, I.K., GUSTI OKA, M. and OKA NURIJAYA, M.G. (1991) New forages species for coconut plantations in Bali. *ACIAR Proceedings No. 32, Forages for Plantations Crops, Bali, 1990*. pp. 41–44.
- SAMARAKOON, S.P., WILSON, J.R. and SHELTON, H.M. (1990) Growth, morphology and nutritive quality of shaded *Stenotaphrum secundatum*, *Axonopus compressus* and *Pennisetum clandestinum*. *Journal of Agricultural Science, Cambridge*, **114**, 161–169.
- SÁNCHEZ, L.F., GARCÍA-MIRAGAYA, J. and CHACÓN, N. (1997) Nitrogen mineralization in soils under grasses and under trees in a protected Venezuelan savanna. *Acta Oecologica*, **18(1)**, 27–37.
- SARMIENTO, G. (1984) *The Ecology of Neotropical Savannas*. (Harvard University Press: Cambridge, MA).
- SARMIENTO, G. (1990) *Las Sabanas Americanas. Aspectos de su Biogeografía, Ecología y Utilización*. (Fondo Editorial Acta Científica Venezolana: Mérida).
- SAS INSTITUTE (1989) *SAS/STATM Guide for personal computers*. (SAS Institute, Inc.: Cary, NC).
- SCHOLES, R.J. and ARCHER, S.R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology & Systematic*, **28**, 517–544.
- SHELTON, H.M., HUMPHREYS, L.R. and BATELLO, C. (1987) Pastures in the plantations of Asia and the Pacific: Performance and prospects. *Tropical Grasslands*, **21**, 159–168.

- SINCLAIR, T.R. and HORIE, T. (1989) Leaf nitrogen, photosynthesis, and crop radiation use efficiency: A review. *Crop Science*, **29**, 90–98.
- SMITH, M.A. and WHITEMAN, P.C. (1983) Evaluation of tropical grasses in increasing shade under coconut canopies. *Experimental Agriculture*, **19**, 153–161.
- STÜR, W.W. (1991) Screening forage species for shade tolerance — a preliminary report. *ACIAR Proceedings No. 32, Forages for Plantations Crops, Bali, 1990*. pp. 58–63.
- STÜR, W.W., HOPKINSON, J.M. and CHEN, C.P. (1998) Experiencia Regional con *Brachiaria*: Asia, el Pacífico Sur y Australia. In: Miles, J.W., Maass, B.L. and do Valle, C.B. (eds) *Brachiaria: Biología, Agronomía y Mejoramiento*. pp. 269–282. (CIAT, EMBRAPA/CNPGC: Cali).
- WILLIAMS, D.G. and BARUCH, Z. (2000) African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biological Invasions*, **2**, 123–140.
- WILSON, J.R. (1990) The eleventh hypothesis: Shade. *Agroforestry Today*, **2**, 14–15.
- WILSON, J.R. (1996) Shade-stimulated growth and nitrogen uptake by pasture grasses in a subtropical environment. *Australian Journal of Agricultural Research*, **47**, 1075–1093.
- WILSON, J.R., CATCHPOLE, V.R. and WEIR, K.L. (1986) Stimulation of growth and nitrogen uptake by shading a rundown green panic pasture on Brigalow clay soil. *Tropical Grasslands*, **20**, 134–143.
- WILSON, J.R., HILL, K., CAMERON, D.M. and SHELTON, H.M. (1990) The growth of *Paspalum notatum* under the shade of a *Eucalyptus grandis* plantation or in full sun. *Tropical Grasslands*, **24**, 24–28.
- WILSON, J.R. and LUDLOW, M.M. (1991) The environment and potential growth of herbage under plantations. *ACIAR Proceedings No. 32, Forages for Plantations Crops, Bali, 1990*. pp. 10–24.
- WILSON, J.R. and WILD, D.W.M. (1991) Improvement of nitrogen nutrition under shading. *ACIAR Proceedings No. 32, Forages for Plantations Crops, Bali, 1990*. pp. 77–82.
- WILSON, J.R. and WILD, D.W.M. (1995) Nitrogen availability and grass yield under shade environments. *ACIAR Proceedings No. 64, Integration of Ruminants in Plantation Systems in South East Asia, North Sumatra, 1994*. pp. 42–48.
- WONG, C.C. (1991) Shade tolerance of tropical forages: A Review. *ACIAR Proceedings No. 32, Forages for Plantations Crops, Bali, 1990*. pp. 64–69.
- WONG, C.C., RAHIM, H. and SHARUDIN, M.A.M. (1985) Shade tolerance potential of some tropical forages for intergration with plantations. I. Grasses. *MARDI Research Bulletin*, **13**, 225–247.
- WONG, C.C. and STÜR, W.W. (1996) Persistence of tropical forage grasses in shaded environments. *Journal of Agricultural Science, Cambridge*, **126**, 151–159.
- ZAR, J.H. (1984) *Biostatistical Analysis*. 2nd Edn. (Prentice-Hall International, Inc.: New Jersey).
- ZIMMER, A.H. and EUCLIDES-FILHO, K. (1997) Brazilian pastures and beef production. *Proceedings of the International Symposium on Animal Production under Grazing, Universidade Federal de Vicosa, MG, Brazil, 1997*. pp. 1–29.

(Received for publication June 7, 2007; accepted November 6, 2007)