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Effects of light intensity on growth, anatomy and forage quality of two tropical grasses (*Brachiaria brizantha* and *Panicum maximum* var. *trichoglume*)

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Abstract

Effects of light intensity on growth, histology and anatomy, and nutritive value were studied in seedlings of two shade tolerant species: *Brachiaria brizantha* (A. Rich) Stapf and *Panicum maximum* var.*trichoglume* (K. Schum.) C.E. Hibbard. They were studied under greenhouse conditions in pots with sandy soil and sufficient N and cut after a growth period of 8 weeks. High light intensity stimulated growth, tillering and yield per tiller and increased stem proportion. It greatly increased number of sclerenchyma cells, their wall thickness in all organs and the content of cell wall constituents. High light intensity also reduced concentrations of total N, NO_3-N and ash appreciably. It reduced digestibility of cell wall constituents in leaf blades but increased it in leaf sheaths and stem, especially in *Panicum*. Variation in sclerenchyma tissue could be associated with variation in percentage of cell wall constituents, but not with variation in cell wall digestibility. The resultant ot these effects of light intensity on composition of organs was a higher digestibility of organic matter of the whole crop at lower light intensity.

Brachiaria was more tolerant to shade than *Panicum* with regard to growth, N-concentration and digestibility, but it accumulated more nitrate.

It was suggested that light intensity may affect forage quality little under low nitrogen supply in the tropics, but effects may be larger at ample nitrogen supply. Individual species may partly divert from this general pattern.

Keywords: plant morphology, histology, anatomy, tissue digestion, N-concentration, cell walls, digestibility, *Brachiaria brizantha* (A. Rich) Stapf, *Panicum maximum* var. *trichoglume* (K. Schum.) C.E. Hibbard.

Introduction

Herbage production under tree crops becomes increasingly popular in some regions of the humid tropics, especially in South-East Asia (Tajuddin, 1991). Growth and nutritive value of herbage are important criteria under such shady conditions (Wilson, 1991). Effects of light intensity on N-concentration and digestibility of dry or organic matter of grass crops varied from positive to negative (Wilson, 1991) but were usually small (Norton *et al.*, 1991). Grass species also differed slightly in their response of nutritive value to light intensity (Norton *et al.*,1991, Wilson, 1991), for unknown reasons. Deinum (1981), however, found a large positive effect of light intensity on digestibility under greenhouse conditions in *Setaria sphacelata* (Schum) Staff and Hubbard. Intake of herbage was often reduced by low light intensity during grass growth (Samarakoon *et al.*, 1990a) for unknown reasons.

In order to reach a better understanding of these variable effects of light intensity on the different parameters of forage quality, an experiment was carried out in which the effects of light intensity on growth, plant anatomy and several quality parameters was investigated under controlled conditions.

Material and methods

Plant growth

Two shade tolerant bunch grasses (Skerman & Riveros, 1990; 't Mannetje & Jones, 1992) were selected for the experiment,i.e. *Brachiaria brizantha* (A. Rich) Stapf and *Panicum maximum* var. *trichoglume* (K. Schum.) C.E. Hibbard), (green panic). They were grown in a ventilated, temperature controlled greenhouse at three radiation levels from sowing onwards.

Daily radiation levels in MJ m^{-2} (400–10000 nm) during the experimental period were on average;

L_1: low light : 2.60 MJ m^{-2}
L_2: medium light: 10.10 MJ m^{-2}
L_3: high light: 17.40 MJ m^{-2}

L_2 was the normal light intensity in the greenhouse representing 65% of outside daylight. L_1 was obtained by shading of L_2, and L_3 by additional light from Philips SON lamps to L_2. L_3 was similar to average daily radiation in the humid tropics. L_1 was low compared to the light intensity used in most shading experiments in the tropics. Radiation levels were lower at the end than at the beginning of the trial because of the progress of the season. Average photoperiod was 15 hours. Average day and night temperatures were 22 and 20°C, respectively, and average relative humidity was 70%.

Plants were grown in 7-litre pots filled with fertile sandy soil. Eight days after sowing seedlings were transplanted (12 plants/pot) on July 22, 1991 and allowed to grow for 7 weeks until September 13. Pots were watered once or twice daily and fertilized frequently to a total of 2.36 g N, 3.28 g K, 0.84 g Ca, 0.30 g P and 0.51 g Mg per pot.

The experiment had a split-plot design with 3 light intensities and 2 replicates. Each plot consisted of 10 pots.

Measurements

Morphological development (length of main tiller, leaf number and tiller number of 3 plants per treatment) was recorded weekly.

Histology and anatomy

At harvest, one main tiller per treatment was preserved in 70% alcohol for subsequent anatomical studies. Phytomer 2 from the top was used for this purpose. This phytomer is composed of the second adult leaf blade from the top, its leaf sheath and the internode below the node bearing leaf 2 (Arber, 1934). These organs have almost certainly completed development, both with regard to shape and secondary cell wall formation and to their adult cell wall digestibility (Deinum, 1992; Nelson, 1992). Leaf blade is formed first, followed by leaf sheath; the stem internode is formed last. Each organ has its intercalary meristem at the base, so the top is oldest. The mid section of leaf blade and leaf sheath and the top of the internode were studied. This top was almost certainly fully grown, but the mid section possibly not yet. These adult organs will show the effects of light intensity during growth to the full extent.

Cross sections of 100 µm were made with a sliding microtome. They were studied with light microscopy up to 10*100 magnification for histological composition, and tissue anatomy before and after 48 hours (in some cases also after 120 hours) in vitro rumen degradation using the section to slide technique of Akin (1982). In vitro degradation was done in the medium of Goering & van Soest (1970) with some meal of forage maize added as additional substrate. Cell wall thickness was measured with an accuracy of about 0.5 µm.

Chemical composition and digestibility

At harvest plants were cut at 10 cm stubble height. Fresh weight was measured and also dry weight after drying at 70°C. Tiller numbers were recorded as well. After drying, the herbage was separated into leaf blades, leaf sheaths, true stems and dead material. Fractions were ground in a hammer mill passing a sieve of 1 mm mesh.

Samples were analyzed for Kjeldahl-N including nitrate-N, for ash and for nitrate with sulfanilamide after reduction to nitrite; cell wall constituents (cwc) and in vitro true digestibility of organic matter were measured according to the procedures of Goering & van Soest (1970). Grass samples of known apparent in vivo digestibility of organic matter in sheep at maintenance level were incorporated to allow conversion of in vitro digestibility into estimated in vivo digestibility (D_{om}). N-concentrations of cell wall constituents were measured in order to calculate cwc free from protein insoluble in neutral detergent (Wilson & Ng, 1975; Deinum & Maassen, 1994).

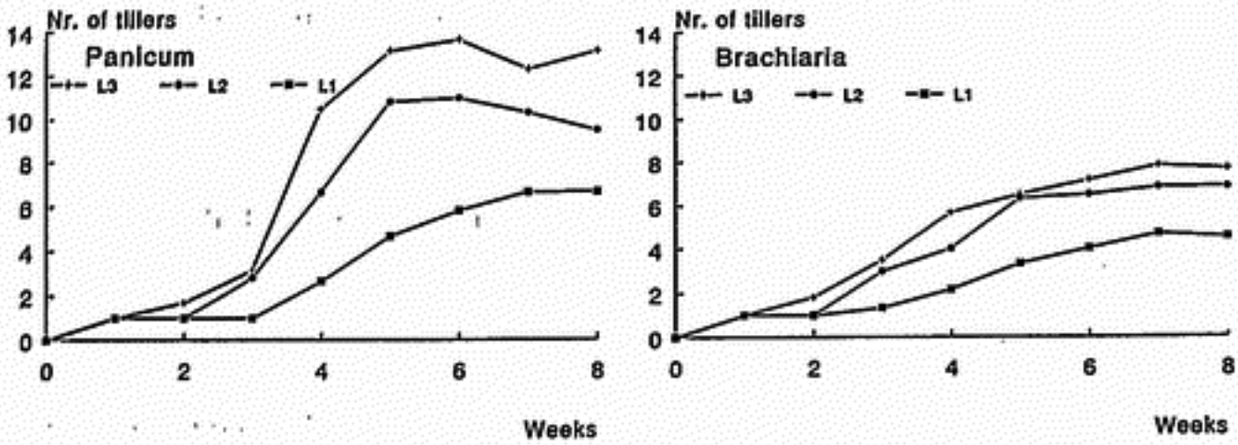


Figure 1. Effect of light intensity on tillering during growth of seedlings of *Brachiaria brizantha* and *Panicum maximum* var. *trichoglume* (number per plant).

Digestibility of protein-free cwc (D_{cwc}) was calculated from in vitro digestibility, ash and cwc. Composition of whole green crop (excluding dead mass) was calculated from the composition and masses of separate fractions.

Results and discussion

Growth and development

The plants grew well; mutual shading occurred during the last three weeks, more in L_3 than in L_1. Main stems reached a length of 1.2 and 1.3 m in *Brachiaria* and *Panicum* at L_3 respectively; they were about 0.2 m shorter at L_1. Main stems produced on average 9 and 12 leaves in *Brachiaria* and *Panicum*, respectively, with little effect of light intensity. *Panicum* showed some inflorescences.

Tillering was stimulated by high light intensity (Figure 1), and was stronger in *Panicum* than in *Brachiaria*. It stopped after about 5 weeks in L_3, possibly because of space limitations, but could continue in L_1. This suggests that tillers were on average somewhat older in L_3 than in L_1, with L_2 in between. These older tillers might be somewhat less nutritious. Number of tillers shorter than 10 cm at harvest was also greater at L_3 (not shown).

Dry matter content was about 10% in L_1 and about 19% in L_3. It was about 1% lower in *Brachiaria* than in *Panicum*. This may be an effect of species, but also of the moment of harvest. Dry mass per pot and per tiller were greatly enhanced by higher light intensity in both species (Table 1).

Proportions of leaf blades were highest in L_1 and in *Brachiaria* (Table 2). Proportion of true stem was greatly reduced by lower light intensity. Within leaves (= blades + sheaths) proportion of leaf sheath declined as well with lower light intensity. This may be associated with etiolation at low light intensity and with the general phenomenon of dominance of leaf blade over leaf sheath and stem under low light.

Table 1. Effect of light intensity on mass of dry matter (g per pot and per tiller) of *Brachiaria brizantha* and *Panicum maximum* var. *trichoglume*.

Species	L_1	L_2	L_3	Mean
Dry mass (g per pot)				
Brachiaria	25.2	62.3	127.0	71.5
Panicum	17.7	82.6	132.6	77.6
Mean	21.5	72.4	129.8	74.6
Dry mass (g per tiller)				
Brachiaria	0.64	1.07	1.84	1.18
Panicum	0.30	1.16	1.27	0.91
Mean	0.47	1.11	1.56	1.05

Significant interaction of shading * species for dry mass per pot: ns; for dry mass per tiller: P=0.021
LSD (P<0.05) for shade treatment per species in dry mass per pot:14.0; for dry mass per tiller: 0.23

Histology, anatomy and tissue digestion

Histological development

Major effects of light intensity were detected in sclerenchyma of both leaf blade, leaf sheath and stem internode. In leaf blade and sheath both number of sclerenchyma bundles and number of cells per bundle increased with higher light intensity. The sclerenchyma ring in stems was also thicker at higher light intensity (Pictures 5 and 7 versus 6 and 8). Other tissues (epidermis, parenchyma, parenchyma bundle sheath and vascular bundles) varied little if at all. Leaf blades and sheaths and stem internodes were somewhat thicker at higher light intensity.

Anatomy

Parenchyma cell walls in all organs were unmeasurably thin, possibly about 0.2 μm

Table 2. Effect of light intensity on morphological composition of dry herbage (% of whole plant) of *Brachiaria brizantha* and *Panicum maximum* var. *trichoglume*

Species and plant part	L_1	L_2	L_3	Mean
Brachiaria				
Leaf blade	74.2	63.3	53.1	63.5
Leaf sheath	20.5	21.7	22.0	21.4
Stem	4.9	13.2	22.7	13.6
Dead	0.4	2.8	2.2	1.8
Panicum				
Leaf blade	54.4	35.7	26.0	38.7
Leaf sheath	25.7	22.6	22.5	23.6
Stem	18.6	38.6	37.2	31.5
Dead	1.3	3.1	14.3	6.2

Significant interaction of shading * species for leaf blade: ns; for leaf sheath: ns; for stem: P=0.01
LSD (P<0.05) for shade treatment per species in leaf blade: 6.04; for leaf sheath: 3.82; for stem: 3.45

(Gordon *et al.*, 1985). Parenchyma bundle sheath cells around the vascular bundles of the leaf blade had walls of about 1 μm thickness.

Thickness of sclerenchyma cell walls was affected by species and shade. Walls were thicker at higher light intensity in all organs, but more so in *Panicum* than in *Brachiaria* (Table 3, Pictures 1–8). Walls of *Brachiaria* were thicker than of *Panicum* in leaf blade, similar in leaf sheath but thinner in stem internode.

Similarly, secondary walls of the lower epidermis of leaf blade (average thickness about 2 μm) were thicker at higher light intensity. Walls of the upper epidermis were somewhat thinner than those of the lower epidermis.

In leaf sheath, secondary walls of the outer and inner epidermis (average thickness also about 2 μm) were again somewhat thicker at higher light intensity. Secondary walls of the cells between the large xylem vessels in vascular bundles (mean thickness also about 2 μm) were also thicker at higher light intensity. However, secondary walls under the cuticula of the outer epidermis were much thicker at higher light intensity in both grasses (up to 6 μm at L_3).

In stem internode, secondary walls of the parenchyma ring were also thicker at higher light intensity (up to 3 μm). Thickness of the epidermal wall below the cuticle was also greater at higher light intensity in both species.

Effects of light intensity on thickness of secondary wall in these tropical grasses were much greater in this trial than effects of temperature in a former one (Wilson *et al.*, 1991).

In conclusion secondary walls were thicker with higher light intensity.

Tissue and cell wall digestion

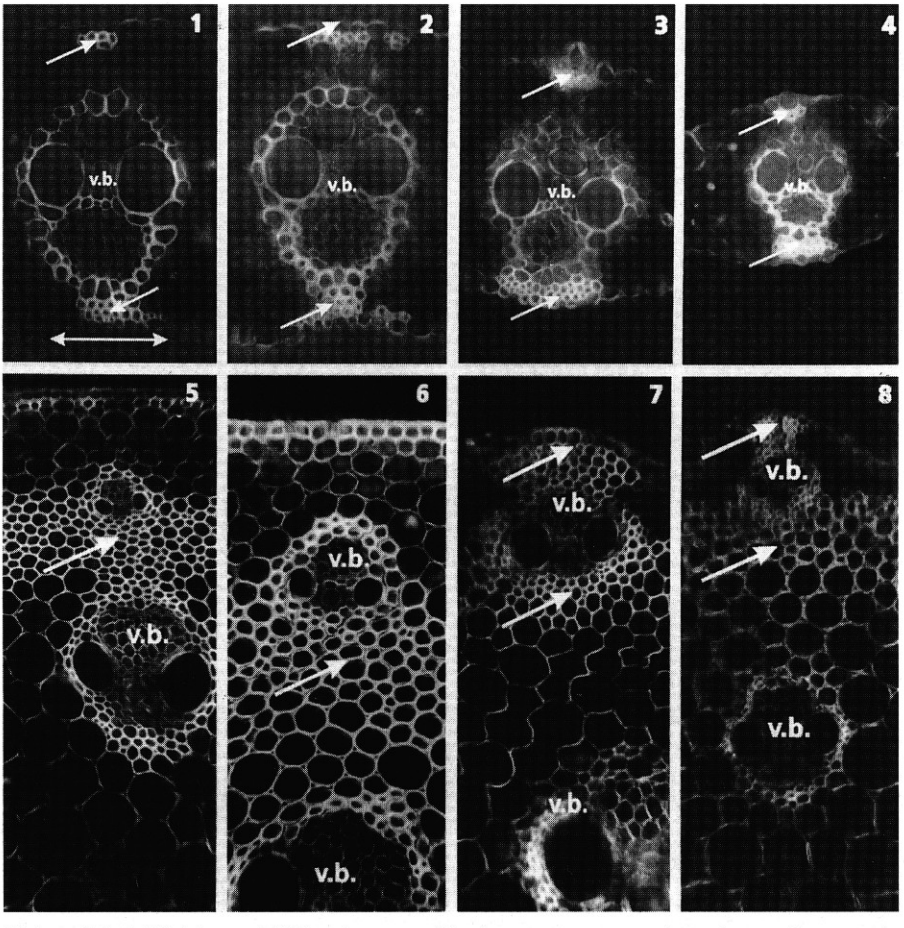
Results can only be described in a broad sense because of incomplete physical accessibility of potentially degradable tissues and walls, even in 100 μm microscopic sections. Only the surfaces of the sections were fully accessible.

Parenchyma of all organs was digested for about 90% after 48 hours, whereas sclerenchyma fibre bundles, vascular bundles and cuticle were retained. Parenchyma developed at low light intensity was digested somewhat better than that produced at high light intensity.

In leaf blades about 20% of parenchyma bundle sheath developed under all light treatments was digested. Secondary walls of epidermis were almost fully digested and secondary walls of sclerenchyma were only partly digested. Digestion of these walls was better in *Brachiaria* than in *Panicum* and increased with higher light intensity during growth.

In leaf sheaths secondary walls of the outer epidermis were only partly digested and somewhat better after low than after high light intensity; the opposite was true for the secondary walls of sclerenchyma which were digested somewhat better after high than after low light intensity. Secondary walls of the inner epidermis were completely digested.

In stem internodes digestion of the parenchyma tissue with secondary walls around the vascular bundles was partly digested, better in *Brachiaria* than in *Panicum* and better in those developed at low than at high light intensity. Secondary



Pictures 1 to 8. Histology of different organs of the two grasses. → = sclerenchyma, vb = vascular bundle. Pictures were taken with polarized light which presents secondary walls better than normal light with histochemical stains. Bar = 100μm.

1 = *Brachiaria* leaf at L_1; 2 = *Brachiaria* leaf at L_3;
3 = *Panicum* leaf at L_1; 4 = *Panicum* leaf at L_3;
5 = *Brachiaria* stem at L_1; 6 = *Brachiaria* stem at L_3;
7 = *Panicum* stem at L_1; 8 = *Panicum* stem at L_3.

wall digestion of the epidermis, of the sclerenchyma and of the parenchyma around the vascular bundles developed at high light intensity was also better than that developed at low light intensity.

Digestion after 120 hours was not much better than after 48 hours. This indicates that digestion was almost completed in 48 hours.

In summary, it can be concluded that digestion of parenchyma was better in material grown at low than at high light intensity. However the thicker secondary walls produced at high light intensity were digested better than the thinner ones produced

Table 3. Effect of light intensity on thickness of sclerenchyma walls (μm) in the different fractions of *Brachiaria brizantha* and *Panicum maximum* var. *trichoglume*.

Species and plant part	L_1	L_2	L_3	Mean
Leaf blade				
Brachiaria	1.6	1.4	3.0	2.0
Panicum	1.3	1.4	2.0	1.6
Mean	1.5	1.4	2.5	1.8
Leaf midrib				
Brachiaria	2.5	2.3	3.8	2.9
Panicum	1.5	2.0	2.5	2.0
Mean	2.0	2.2	3.2	2.4
Leaf sheath				
Brachiaria	2.8	2.9	3.5	3.1
Panicum	1.6	3.3	3.5	2.8
Mean	2.2	3.1	3.5	2.9
Stem internode				
Brachiaria	0.8	1.1	2.2	1.4
Panicum	1.1	2.9	3.8	2.6
Mean	1.0	2.0	3.0	2.0

Significant interaction for shade * species for leaf blade: ns; leaf midrib: ns; leaf sheath: ns and stem internode: $P = 0.03$.
LSD ($P<0.05$) for shading effects within species in leaf blade:0.61; leaf midrib: 0.51; leaf sheath: 0.77; stem internode:0.89.

at low light intensity. This was more pronounced in *Panicum* than in *Brachiaria*.

Chemical composition and digestibility

Total N

Total N concentration was reduced by growth at higher light intensity in all fractions (Table 4). It was higher in *Brachiaria* than in *Panicum*, associated with its lower yield.

Leaf blades had highest N concentration. *Panicum* leaves were richer in N than *Brachiaria* leaves. Stems of *Panicum* were lower in N concentration which may be associated with their greater development and weight. N-yield was highest in L_3 and amounted to almost 80% of N-supply.

Ash concentrations (not presented) were also lower at higher light intensity.

Nitrate-N concentrations (not presented) of all fractions were much lower at higher light intensity and were highest in leaf sheaths and true stems in agreement with the literature (a.o. Deinum, 1981). *Brachiaria* accumulated more nitrate than *Panicum*. Nitrate concentration in herbage at L_1 and L_2 exceeded dangerous levels for animal health (about 0.2% NO_3-N). Mean organic N-concentration (= total-N minus nitrate-N) of the whole crop was 2.5, 2.0 and 1.4% in L_1, L_2 and L_3 respectively.

Table 4. Effect of light intensity on total N-concentration (% of dry matter) in the different fractions of *Brachiaria brizantha* and *Panicum maximum* var. *trichoglume*.

Species and plant part	L_1	L_2	L_3	Mean
Leaf blade				
Brachiaria	3.68	3.09	2.08	2.95
Panicum	4.19	3.41	2.48	3.36
Mean	3.94	3.25	2.28	3.16
Leaf sheath				
Brachiaria	2.74	2.18	1.00	1.97
Panicum	3.41	1.65	1.01	2.00
Mean	3.08	1.92	1.01	2.00
Stem				
Brachiaria	2.94	2.31	0.98	2.07
Panicum	3.04	1.14	0.69	1.62
Mean	3.00	1.73	0.84	1.85
Whole plant				
Brachiaria	3.45	2.78	1.58	2.60
Panicum	3.77	2.09	1.32	2.39
Mean	3.61	2.44	1.45	2.50

Significant interaction of shading * species in leaf blade: ns; for leaf sheath: $P<0.001$; for stem: $P=0.002$; for whole: $P=0.001$.
LSD ($P=0.05$) of shading effect within species for leaf blade: 0.28; for leaf sheath: 0.13; for stem; 0.18; for whole plant: 0.12.

Cell wall constituents

Percentages of protein-free cwc were low at 58% compared to about 75% normally found in the tropics (Norton *et al.*, 1991). They increased with higher light intensity in all fractions (Table 5). Concentrations were lowest in leaf blades and higher in leaf sheaths and true stems. *Brachiaria* and *Panicum* had similar concentrations in leaf blade and leaf sheath, but *Panicum* had higher concentrations in stems which is possibly associated with its higher stem weight. There were clear interactions in leaf sheath and stem mainly caused by the L_2 treatment: L_2 gave similar values as L_1 in *Brachiaria*, but similar values as L_3 in *Panicum*.

These effects of light intensity on the concentration of cell wall constituents are opposite to the effects on protein concentrations (= organic-N * 6.25). Such results were also found in C_4 (Wilson, 1973) and C_3 and C_4 grasses (Kephart and Buxton, 1993) low in sugars where a high N-concentration is associated with low %cwc. This is supported in our experiment by the almost constant concentration of about 15% of not measured cell solubles (non-structural carbohydrates, organic acids, fats). However in temperate grasses that accumulate sugars, a high N-concentration is associated with lower sugar concentration but similar %cwc.

The higher stem fraction in *Panicum* and its higher %cwc caused a higher %cwc in whole crop of this species.

Table 5. Effect of light intensity on protein-free cell wall constituents (% of dry matter) in the different fractions of *Brachiaria brizantha* and *Panicum maximum* var. *trichoglume*.

Species and plant part	L_1	L_2	L_3	Mean
Leaf blade				
Brachiaria	45.2	49.4	55.6	50.0
Panicum	40.9	48.5	56.8	48.7
Mean	43.0	49.0	56.2	49.4
Leaf sheath				
Brachiaria	61.0	63.0	71.0	65.0
Panicum	54.3	68.5	73.5	65.4
Mean	57.7	65.8	72.3	65.2
Stem				
Brachiaria	60.6	64.4	75.2	66.7
Panicum	61.7	77.9	81.6	73.7
Mean	61.2	71.2	78.4	70.2
Whole plant				
Brachiaria	49.1	54.3	63.4	55.6
Panicum	48.0	64.4	71.6	61.3
Mean	48.6	59.4	67.5	58.5

Significant interaction of shading * species for leaf blade: ns; for leaf sheath; P=0.004; for stem: P=0.001; for whole plant: P= 0.013.
LSD (P=0.05) for shade treatment per species in leaf blade: 3.77; for leaf sheath:2.44; for stem: 1.62; for whole plant were; 3.45.

The higher %cwc at higher light intensity can be associated with the greater quantity of sclerenchyma: more cells and thicker walls at higher light intensity (Pictures 1–8 and Table 3). Assimilates not used for protein formation have apparently been used for sclerenchyma formation and for secondary wall thickening. Kephart and Buxton (1993) speculated already on this possibility.

Digestibility of cell wall constituents

Effects of light intensity on D_{cwc} were variable (Table 6).

Higher light intensity reduced D_{cwc} of leaf blades. In leaf sheaths it was increased from L_1 to L_2 but was decreased slightly from L_2 to L_3. D_{cwc} of true stems was not affected in *Brachiaria* but in *Panicum* it was increased considerably from L_1 to L_2. *Brachiaria* and *Panicum* showed similar D_{cwc} of leaf, but D_{cwc} of leaf sheaths and true stems were highest in *Brachiaria*, resulting in the better D_{cwc} in the whole crop of *Brachiaria*.

There was no effect of light intensity on D_{cwc} of the whole crop in *Brachiaria*, but a large positive effect from L_1 to L_2 in *Panicum*. Smaller but also variable effects of light intensity on D_{cwc} could be calculated from the experiment of Samarakoon *et al.*, (1990b) with three mat-forming species grown in pots.

Effects of light intensity on D_{cwc} were smaller in this trial than effects of temperature in a former trial (Wilson *et al.*, 1991), opposite to effects on cwc%.

Table 6. Effect of light intensity on digestibility of cell wall constituents (%) in the different fractions of *Brachiaria brizantha* and *Panicum maximum* var. *trichoglume*.

Species and plant part	L_1	L_2	L_3	Mean
Leaf blade				
Brachiaria	74.7	69.1	65.5	69.7
Panicum	74.1	68.9	67.8	70.3
Mean	74.4	69.0	66.7	70.0
Leaf sheath				
Brachiaria	44.3	56.9	53.9	51.7
Panicum	40.5	49.7	46.9	45.7
Mean	42.4	53.3	50.4	48.7
Stem				
Brachiaria	72.0	70.8	72.7	71.8
Panicum	37.7	61.8	59.7	53.0
Mean	54.9	66.3	66.2	62.4
Whole plant				
Brachiaria	66.6	66.2	64.4	65.7
Panicum	55.1	60.4	58.0	57.8
Mean	60.9	63.3	61.2	61.8

Significant interaction of shading * species for leaf blade: ns; for leaf sheath: ns; for stem: P=0.012; for whole plant: P= 0.099.
LSD (P=0.05) for shade treatment per species in leaf blade: 3.92; for leaf sheath: 2.85; for stem: 7.52; for whole plant: 3.90.

Apparent digestibility of organic matter

The separate effects of light intensity and species on % cwc and D_{cwc} culminate in their effects on D_{om}.

Whole plants had a high D_{om} for tropical grass (65%; Table 7), compared to Norton *et al.*(1991). Digestibility of leaf blades was reduced by higher light intensity, but digestibility of leaf sheaths and of true stems reacted variably to light intensity. *Brachiaria* sheaths and *Panicum* stems showed low values at L_1 compared to L_2 and L_3.

D_{om} of whole crop declined with higher light intensity in both grasses, similar to results of Kephart and Buxton (1993) in some C_3 and C_4 grasses, but opposite to the results in a former trial in which D_{om} of *Seteria sphacelata* increased with higher light intensity (Deinum, 1981).

Panicum was less digestible than *Brachiaria*. Leaf blades had the highest and leaf sheaths the lowest digestibility. Stems were intermediate.

General discussion

Chemical composition and digestibility of the herbage is the cumulative expression of processes in the plant during growth. A great deal of the variation in chemical

Table 7. Effect of light intensity on apparent digestibility of organic matter (%D_{om}) in the different fractions of *Brachiaria brizantha* and *Panicum maximum* var. *trichoglume*.

Species an plant part	L_1	L_2	L_3	Mean
Leaf blade				
Brachiaria	77.1	73.2	69.5	73.2
Panicum	78.0	73.6	70.3	73.6
Mean	77.6	73.4	69.9	73.6
Leaf sheath				
Brachiaria	50.8	59.8	55.0	55.2
Panicum	51.3	52.0	48.3	50.5
Mean	51.1	55.9	51.7	52.7
Stem				
Brachiaria	70.8	69.1	68.4	69.4
Panicum	45.6	58.4	55.9	53.3
Mean	58.2	63.8	62.2	61.4
Whole plant				
Brachiaria	71.4	69.7	66.0	69.0
Panicum	65.2	62.4	58.2	61.9
Mean	68.3	66.1	62.1	65.5

Significant interaction of shading * species for leaf blade; ns; for leaf sheath: P=0.007; for stem: P=0.023; for whole plant: ns.
LSD (P<0.05) for shade treatment per species in leaf blade: 2.23; for leaf sheath: 2.11; for stem; 5.56; for whole plant: 3.31.

composition may therefore be associated with the development and growth of the grasses. However, our results show that it is still difficult to relate chemical composition and digestibility with histological and anatomical development. This was mainly due to

- the variable physical accessibility of cell walls to microbial digestion in microscopic sections and in meals (Wilson & Mertens, 1995),
- different sample size (young adult organs from the main tiller per treatment for histological studies versus the bulk of younger and older organs for chemical studies).
- variable effects of light intensity on D_{cwc} of sclerenchyma in different organs and species.

The tables show that there were often significant interactions of shading*species for the different parameters (growth and nutritive value), indicating that each species has its own response to shading.

Shading reduced growth and increased N-concentration and D_{om} in both species. However, the *Brachiaria* seedlings revealed in general better tolerance to shading than *Panicum* with regard to growth (Table 1), N-concentration (Table 4) and D_{om} (Table 6 and 7), but they accumulated more nitrate. Shade tolerance of regrowth after cutting could not be studied in this trial.

Results were partly in line with earlier trials with tropical grasses grown in pots

(Deinum, 1981). Shading had a larger and more positive effect on both N-concentration and D_{om} in this trial than in most other published research (Wilson, 1982; Norton *et al.*, 1991). The very low light intensity of the L_1-treatment compared to the lowest light intensity treatments in published trials may also partly be responsible for our larger effects. Negative effects of shading on D_{om} have also been found (e.g. Deinum, 1981; Deinum *et al.*, 1968).

Light intensity and N-supply usually have synergistic effects on growth and dry matter production but antagonistic effects on N-concentration and D_{om} of temperate and tropical grasses (e.g. Deinum *et. al.*, 1968, Deinum, 1981), and possibly also on cell wall development. N-concentration is the quotient of N-yield in herbage and dry matter yield and consequently the result of the processes of N-uptake and dry matter production. Higher N-supply usually stimulates N-uptake more than dry matter production and higher light intensity stimulates dry matter production more than N-uptake. Hence it is not surprising that grass grown at lower light intensity resembles grass grown at higher N-supply. Such processes are usually more pronounced in pot experiments than in field trials because of less mutual shading in pot experiments and of smaller soil volume. Hence effects of light intensity and N-supply on forage quality are usually smallest in field trials. This is apparent in the work of Samarakoon *et al.*, (1990,a,b). It can also be inferred from their work that with limited N-supply, N-yield and dry matter yield were often higher at low than at high light intensity, possibly because of smaller investments of N and assimilates in root and stubble growth.

It is suggested that small effects of shade on forage quality prevail under the often limited N supply under shade trees, but that larger effects will be found at abundant N supplies as in our experiment when harvested at the same age. However, if herbage is harvested or grazed at the same yield, grass grown in the shade is older and may possibly be of poorer quality. These hypotheses may be tested best under field conditions in the humid tropics with wide ranges of N-supply and shading.

These phenomena will occur in general, especially for N- and cwc-concentration. Average effects of light intensity on D_{cwc} were small. However they varied from positive in *Setaria sphacelata* (Deinum, 1981), no effect in *Brachiaria brizantha*, to negative in *Panicum maximum* var *trichoglume* (this paper) which may be associated with different masses of sclerenchyma, cell wall and its degradability.

Since effects of shade are relatively small under field conditions in comparison to interspecific differences it is recommended to search for shade tolerant species with good forage quality, in agreement with Norton *et al.*, (1991).

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