Leaf morphogenesis and site filling in the establishment period in three Guinea grass (*Panicum maximum*) cultivars

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Abstract

In two short term experiments, descriptive data for leaf number per main tiller, leaf appearance rate, leaf final length, leaf elongation rate, tiller number and tiller site filling were collected from three cultivars of Guinea grass (*Panicum maximum*, Jacq.) Aruana, Mombaça, and Tanzânia, recently released by research institutions in Brazil. The first experiment (E1) was carried out in a growth cabinet, with a constant temperature of 28°C, humidity around 80%, constant light of 350 μm/m^2/s and photoperiod of 24 h, and included three levels of defoliation (50 mm, 200 mm and uncut). The second experiment (E2) was carried out in a glasshouse with temperature between 15 and 25°C and natural day light from mid September to mid December. Measurements spanned the establishment period, until plants were four (E1) and three months of age (E2). Cv. Mombaça had a faster leaf elongation rate (77.2 mm leaf tiller/day) and produced longer leaves (752 mm) than cv. Tanzânia (73.6 mm leaf tiller/day and 519 mm) and Aruana (67.2 mm leaf tiller/day and 426 mm). Aruana had a higher number of leaves on the main stem after 12 weeks growth (18 and 13.9) than cv. Mombaça (14.8 and 11.9) in E1 and E2, respectively. Severe defoliation depressed leaf elongation rate, mainly in the first week of regrowth in cv. Mombaça and Tanzânia. All cultivars had more rapid leaf appearance in E1 than in E2, and more tillers/plant in the second experiment. The site filling ratio was 0.167 in E1 and 0.227 in E2. The data presented would be suitable for construction of a modular growth simulation for Guinea grass.

Additional key words: Panicum maximum, *Guinea grass, morphogenesis, phyllochron, site filling*

Introduction

Tropical grasses are capable of yields of 50–70 t DM/ha, compared with less than 25 t DM/ha in temperate grasses (Cooper, 1970). Agronomic research on tropical grasses to date has focussed on effect of defoliation height, defoliation frequency, timing of defoliation, and fertiliser application rate to optimise yield (e.g. Pacheco *et al.*, 1984; Favoretto *et al.*, 1987), and there have been few studies (Pinto *et al*, 1994; Gomide, 1997; Santos, 1997) on basic aspects of plant morphogenesis in tropical grasses. By contrast, detailed study of the development, growth and senescence of leaves and tillers has made a major contribution to understanding of the scope for manipulating production in temperate grasses (Hodgson, 1990). We were interested to gather information that would advance understanding of tropical grass swards in a similar way. Hence, the main objective of this work was to collect data on aspects of leaf morphogenesis during the establishment period in three cultivars of Guinea grass (*Panicum maximum* Jacq), a species widely used in tropical pastures. One application for this data would be in fine-tuning grazing systems for optimum plant and animal performance. A possible future application would be in extending models of leaf production and senescence (Durand *et al.*, 1998) for tropical grasses.

Materials and Methods

Two experiments were carried out in pots (E1 and E2), with three cultivars of *Panicum maximum* recently released in Brazil: Aruana, Mombaça and Tanzânia.

The plants in E1 were grown in a growth cabinet with temperature between 28-30°C, humidity around 80%, 24h photoperiod, and average light intensity of 350 μmoles/m^2/s, for 16 weeks between April and August. Two-litre pots were filled with sand and fertilised (6 g/pot) with a controlled release fertiliser (15% N, 4.8% P, 10.8% K, 1.2% Mg, 3.0% S, 0.4% Ca plus trace elements, B, Cu, Fe, Mn, Mo and Zn). Seven days after germination, seedlings were thinned to four of similar size per pot. The first harvest was made after 28 days, followed by three further harvests at 21 day intervals. There were three defoliation levels: low cut (50 mm height), high cut (200 mm height) and no defoliation.

The experiment therefore was a 3 x 3 factorial design with four blocked replicates. E2 was conducted in a glass house over 12 weeks from mid September to mid December in natural daylight, with temperature ranging between 15 and 25°C. Seeds were germinated in a tray and after two weeks, four similar size seedlings were transplanted to two litre pots filled with the same growth medium as in E1. All plants were allowed to grow undefoliated and there were five replicates of the three cultivars in a completely randomised design. In E1, one plant per pot was selected for leaf measurements and in E2, two plants per pot were sampled in an attempt to decrease variance in the data. In both trials plants were watered daily with tap water and with 200 ml Hoagland's nutritient solution applied weekly per pot.

Twice weekly, in both experiments, the number of leaves present on the main tiller (including the elongating leaf), and the number of tillers per plant were counted, and the leaf length (mm) of all leaves on the main tiller was measured. From these data, tiller appearance rate, leaf appearance rate (LAR), leaf elongation rate (LER), final length of each leaf, and cumulative number of leaves which had appeared on each main tiller were calculated on a weekly basis. The phyllochron (expressed in growing degree days (GDD), $T_b = 15°C$) was calculated as the inverse of the slope of the regression of cumulative leaf number on GDD. Site filling (Davies and Thomas, 1983) was calculated as the regression slope of $\log_e$ (number of tillers per plant) on cumulative number of leaves on each main tiller.

Results

The phyllochron increased over the course of the experiment in E1, but remained constant in E2, for all three cultivars (Fig. 1a, 1b, and 1c). Accordingly, three regression lines were fitted to calculate the phyllochron for different time periods in E1 (0 - 400, 500 - 1200, and 1300 - 1550 cumulative GDD), and a single regression line was fitted to calculate phyllochron in E2 (Fig. 1a, 1b, and 1c). The same pattern of development was apparent in E1, for all cultivars, with a low value until 400 degree days, and a higher value until the end. For all three time periods in E1, the values for cv. Aruana were smaller than for cv. Mombaça (38, 107 and 151 GDD compared with 42, 182 and 263 GDD, respectively). In E2, cv. Aruana again had shorter phyllochron (62 GDD), than cv. Mombaça (75 GDD). Values for cv. Tanzânia were intermediate in both E1 and E2

LER in E1 was highest at week 4 for all three cultivars, and lower thereafter (Table 1). In E2, LER increased over time, and average LER was lower than in E1 for all cultivars (Table 1). However, LER of cv.

Table 1. Leaf elongation rate, cumulative leaf number and number of green leaves per main tiller over the experimental period in three Guinea grass cultivars (Aruana, Mombaça and Tanzânia).

		Exp't 1				Exp't 2			
	Week	Aruana	Mombaça	Tanzânia	s.e.m.	Aruana	Mombaça	Tanzânia	s.e.m.
	2	14.5 a	12.6 a	14.3 a	0.76	5.0 b	6.0 a	5.9 a	0.14
Leaf Elongation Rate	4	94.3 b	114.1 a	106.3 ab	5.23	30.6 a	34.1 a	34.4 a	1.16
(mm leaves/d/main tiller)	8	70.5 a	67.4 a	71.7 a	3.22	62.1 a	54.8 b	50.2 b	1.40
	12	32.0 b	76.9 a	71.6 a	7.91	73.6 a	64.0 ab	59.3 b	3.89
12 weeks average		64.6 b	77.1 a	73.5 a	2.33	48.8 a	45.6 b	42.1 c	0.83
	2	4.5 a	4.3 a	4.5 a	0.15	3.0 a	3.0 a	3.0 a	0.0
Cumulative Leaf Number	4	9.5 a	9.0 a	9.5 a	0.14	5.0 b	4.6 c	5.4 a	0.10
(main tiller)	8	14.5 a	12.0 b	13.8 a	0.34	9.8 a	8.6 b	10.0 a	0.13
	12	18.0 a	14.8 b	16.8 a	0.47	13.9 a	12.0 b	14.0 a	0.18
	2	4.5 a	4.3 a	4.5 a	0.15	3.0 a	3.0 a	3.0 a	0.0
Total green leaves	4	3.0 b	4.0 ab	4.3 a	0.33	5.0 b	4.6 c	5.4 a	0.10
(main tiller)	8	4.3 a	3.5 a	4.3 a	0.37	6.8 a	6.4 a	6.7 a	0.14
	12	5.3 a	3.5 b	4.0 ab	0.44	6.8 a	6.3 b	6.8 a	0.12
12 weeks average		4.9 a	4.2 a	4.8 a	0.23	6.0 b	5.8 b	6.3 a	0.07

Means, within each row (and within each experiment) followed by the same letter, are not significantly different at P<0.05.

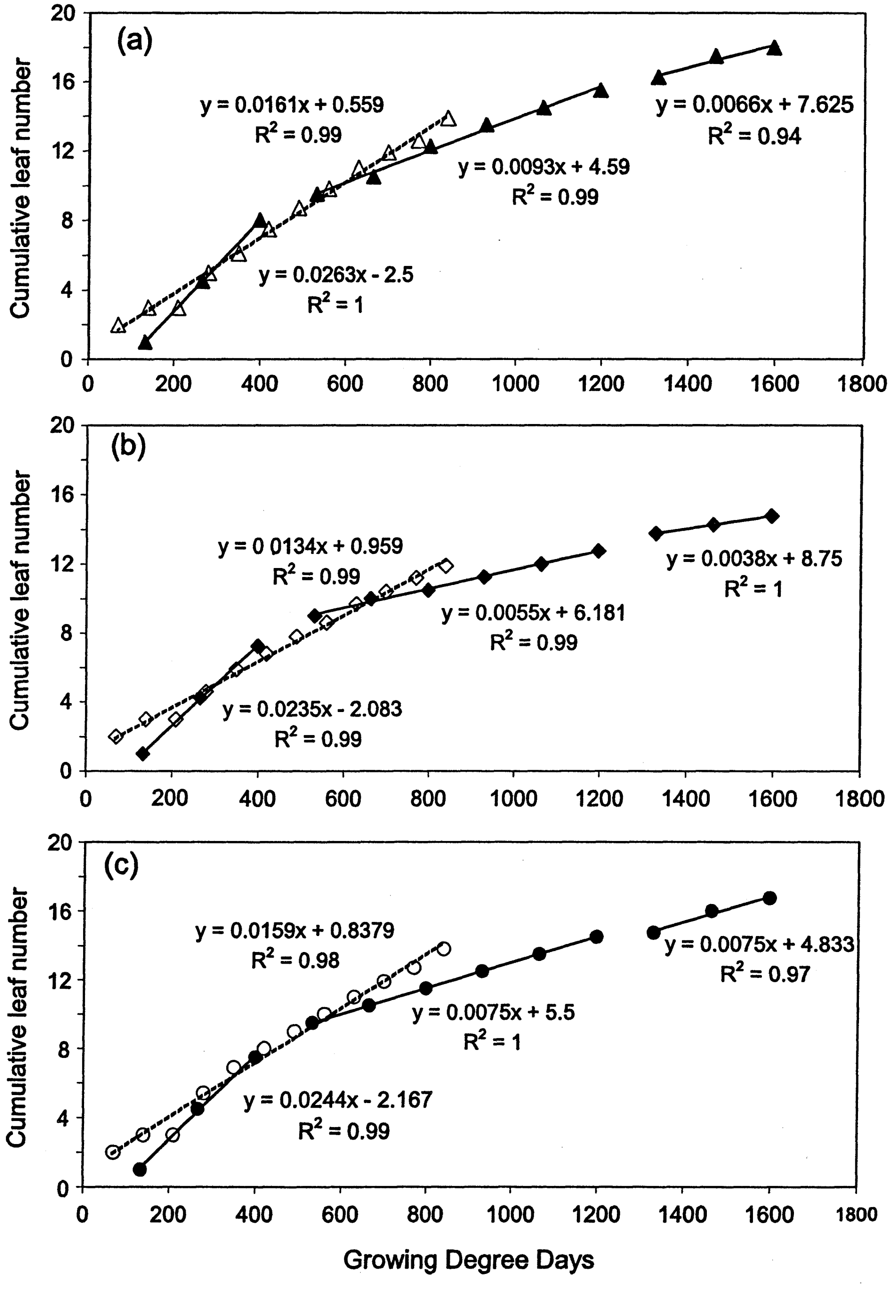

Figure 1. Leaf and tiller appearance on the main tiller for three Guinea grass cultivars (a) Aruana, (b) Mombaça and (c) Tanzânia in E1 (solid line) and E2 (dotted line). Inverse of the slope coefficients is the phyllochron.

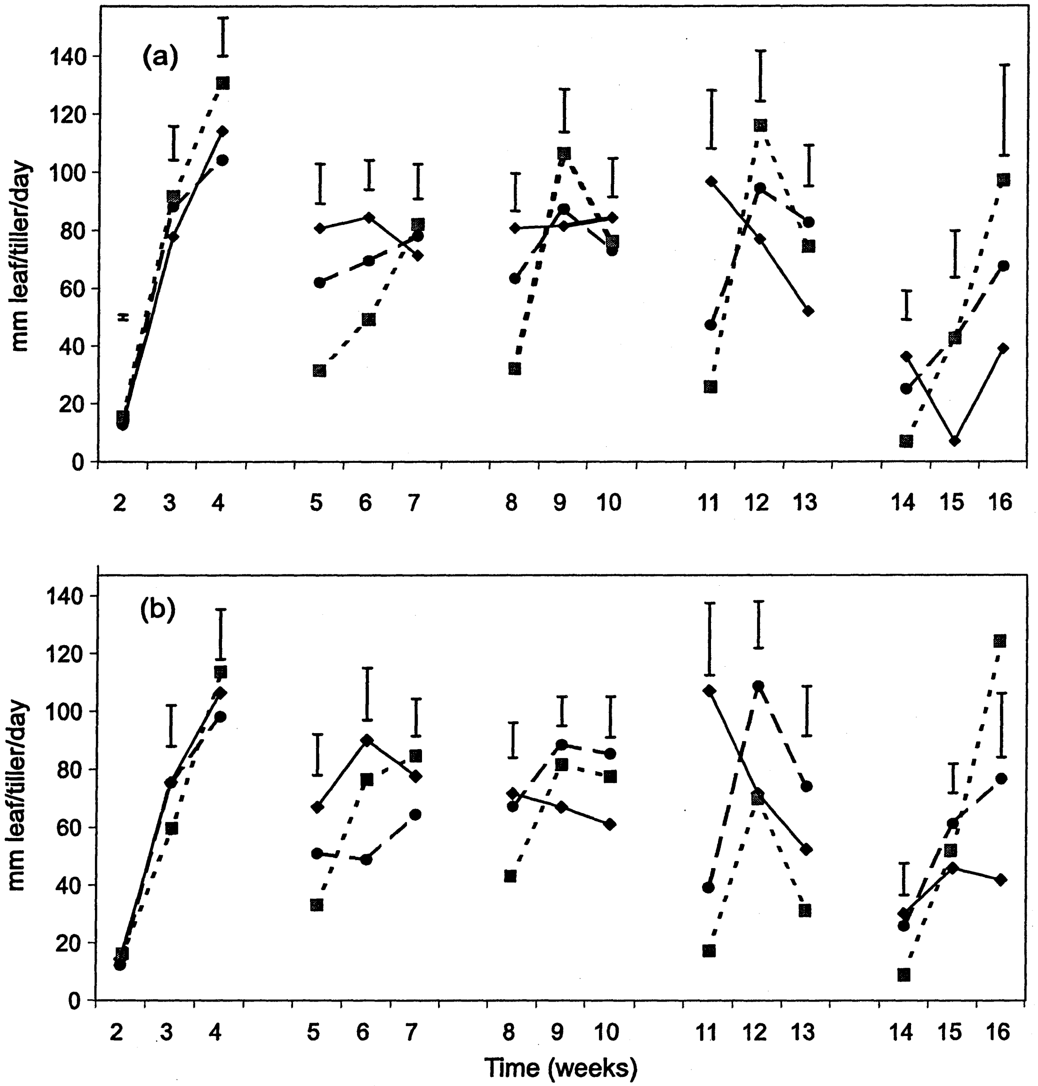

Figure 2. **Effect of three defoliation levels, low cut (- - - - - - -), high cut (– – – – –) and undefoliated (————), on leaf elongation rate (mm/leaf/main tiller/day) in two Guinea grass cultivars, (a) Mombaça and (b) Tanzânia. Bars are values of s.e.m. for each week.**

Aruana seemed to be reduced less in E2 (32% reduction) than in cv. Mombaça and Tanzânia (reductions of 64.8% and 74.6%, respectively). Data on cutting height effect on LER are presented only for two cultivars, Mombaça and Tanzânia (Fig. 2a and 2b), because cv. Aruana showed a different growth form from the other two cultivars, characterised by internode elongation on the main tiller with smaller daughter tillers at most axillary bud sites. For cv. Mombaça and Tanzânia, severe defoliation reduced LER in the week after defoliation. In subsequent weeks differences between cultivars were small and inconsistent, though undefoliated plants generally had the lowest LER in week 3 and severely defoliated plants of cv. Mombaça had comparatively high LER (Fig. 2a and 2b). In Mombaça, under severe defoliation, all main tillers had died by cut 4, and 75% by cut 4 under lax defoliation. In cv. Tanzânia all main tillers died after cut 3 in the low cut treatment, and none in the lax cut treatment. Wherever a main tiller died, an older primary tiller was randomly selected to continue measurement of LER.

Cv. Aruana produced more leaves than cv. Mombaça in E1 and E2 with cv. Tanzânia intermediate, ($P < 0.05$), although there was a smaller difference between cultivars in E2 than in E1 (Table 1). The average number of green leaves per main tiller was 4.6 in E1, but was 6.1 in E2 (Table 1), suggesting that leaf senescence was lower in E2 than in E1.

Final leaf length increased with level of insertion for the greater part of both experiments, with cv. Mombaça consistently having a longer final leaf length than cv. Tanzânia (Fig. 3). In E1, leaf length was similar for all cultivars until L7 (Fig. 3a). From then on, cv. Mombaça had longer leaves than the other two cultivars ($P < 0.05$). The decline in leaf length in cv. Aruana from L14 occurred in association with the initiation of flowering,

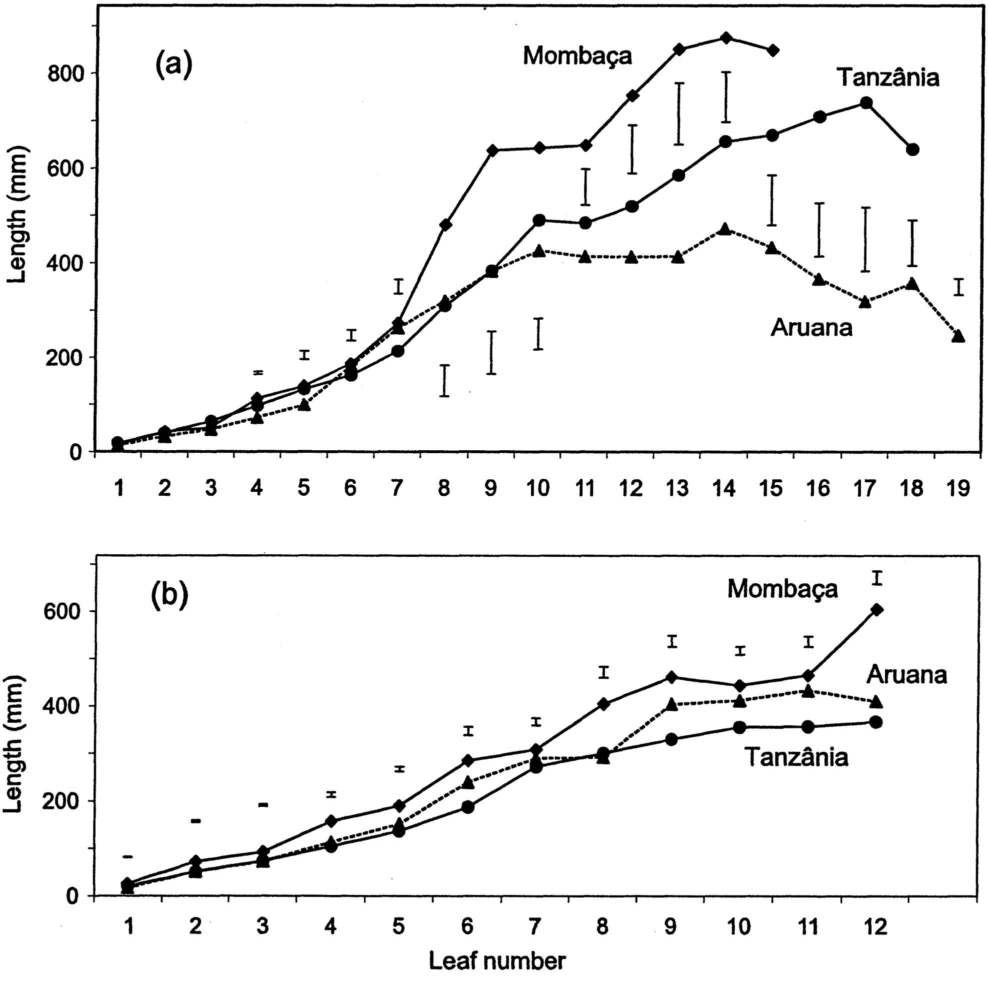

Figure 3. Leaf length on main tiller of three Guinea grass cultivars, Aruana, Mombaça and Tanzânia in two experiments, (a) E1 and (b) E2. Bars are values of s.e.m. for each leaf.

with the last few leaves before the flag leaf progressively decreasing in size (Fig. 3a). In E1, the main tiller in all plants monitored in cv. Mombaça died before the end of the trial, thus the final leaf length shown at L14 (Fig. 3a) represented older primary tillers. Cv. Tanzânia produced more leaves in the same time period, with the longest at L17 (Fig. 3a).

Average site filling (Davies and Thomas, 1983) over the whole experiment was fitted by regression of $\log_e$ tiller number per plant on cumulative main stem leaf number. Values were higher in E2 than in E1 and tended to be lower in cv. Tanzânia than in the other two cultivars (Table 2). These plots showed varying degrees of non linearity and one example is given for cv. Mombaça (Fig. 4a and 4b), but as this issue was not explored further, data for the other cultivars are not presented.

Table 2. Regression of $\log_e$ tiller number per plant on cumulative number of leaves on the main tiller. The slope coefficient is an average site filling value for the whole experiment.

Cultivar	Exp't	Regression equation	R^2
Aruana	E1	Y = – 0.0573 + 0.1983X	0.9307
	E2	Y = - 0.8864 + 0.2813X	0.9765
Mombaça	E1	Y = - 0.3324 + 0.1859 X	0.9167
	E2	Y = - 0.8895 + 0.2814 X	0.9762
Tanzânia	E1	Y = - 0.0051 + 0.1526 X	0.7835
	E2	Y = - 0.8112 + 0.2493 X	0.9665

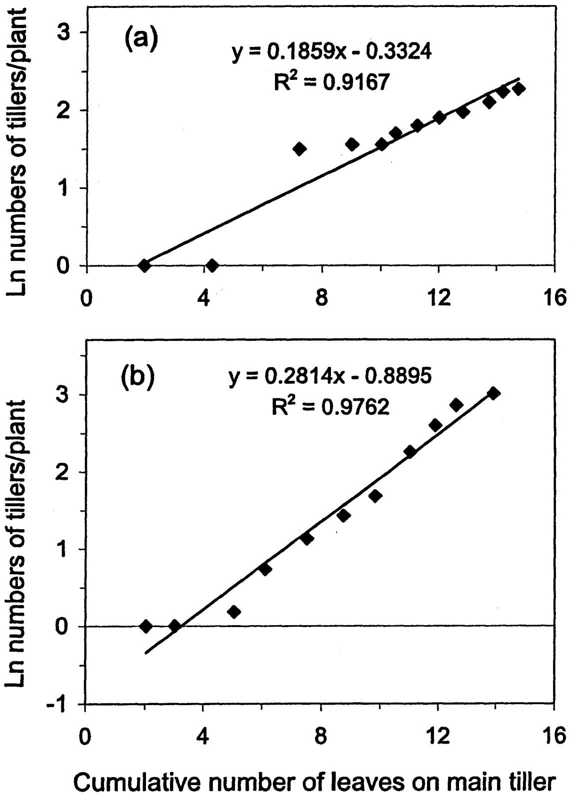

Figure 4. Site filling in *Panicum maximum*, Guinea grass cultivar Mombaça, in two experiments (a) E1 and (b) E2. Slope coefficients of equations are values of site filling.

Discussion

The progressive increase in leaf length as plants matured (Fig. 3a and 3b) provides a probable explanation for the increase in phyllochron as E1 progressed (Fig. 1a, b, and c). Similar differences in leaf length with level of insertion were found in *P. maximum* cv. 'Green panic' by Wilson (1976). He found morphological and anatomical differences between leaves, with leaf length increasing progressively up to leaf ten, then decreasing. In E2, increase in phyllochron as plants matured would have been counterbalanced by seasonal increase in day length, and this probably explains the constant phyllochron for E2 (Fig. 1).

That severe defoliation appeared to affect recovery of cv. Tanzânia plants to a greater extent than plants of cv. Mombaça is an indication that some variability in grazing tolerance may exist in the species and this would be interesting to explore further. However, it is clear that cutting to 50 mm every three weeks is not an appropriate management for *P. maximum,* due to the large tiller size, a point also made by Humphreys (1991). Nor can it be assumed that tillers in different hierarchical positions have similar LER. Gomide (1997) found a higher LER on primary tillers than on the main tiller in four Guinea grass cultivars.

LER in grasses is regarded as a sensitive indicator of environmental effects acting on plants, and of plant vigour, and is also a major determinant of productivity. The higher LER in E1 than E2 (Table 1) is likely due to the higher temperature in the growth cabinet (E1) than in the glasshouse (E2). Silva (1995), suggested that water and temperature are the most important climatic factors affecting *P. maximum* distribution, and most genotypes of this species appear in tropical areas with high temperatures and precipitation (between latitude 20°N and 20°S). These conditions were more closely simulated in E1 than E2. It seems that in E1 the potential of these plants could be expressed and the differences between cultivars were, consequently, more evident.

Other effects probably arising from the temperature difference were seen. In E1, the mean number of green leaves on the main tiller was 4.6, similar to the value 4.4 obtained by Gomide (1997), who studied four *P. maximum* cultivars. By contrast in E2, the average was significantly higher at 6.2 ($P < 0.05$), indicating that in E1 senescence was higher than in E2. Similarly, site filling was low in E1 compared with E2 (Fig. 4, Table 2). These differences in behaviour between experiments are much more pronounced than the cultivar and cutting height effects within experiments and suggest that even though *P. maximum* is able to grow rapidly at high temperatures, such responses leave the plant physiologically stressed due to excess of carbon demand over supply. This is an effect of high temperature often seen in temperate grasses, also (Chatterton *et al.*, 1989).

One of the objectives of these experiments was to identify opportunities for manipulation of *P. maximum* swards with a view to improving persistence and productivity in the field. There is always a question as to how closely results from glasshouse trials describe the dynamics of field swards. In these two experiments, the plant density was 4-6 times greater than that typically encountered in field swards, and individual plants were correspondingly smaller. For example, Andrade (1987) recorded an average of 317 tillers/m^2 with a mean tiller weight of 5.26 g in field swards whereas the corresponding value for E1 was 3300 tillers/m^2 with the mean tiller weight being 0.76g. Also, in E1 light intensity was about 20% of that encountered in the natural environment of these plants at mid day. Maintaining continuous light boosted the daily energy received, but the 24 hour photoperiod would have had subtle effects on plant physiological responses.

However, comparative differences between cultivars in leaf length, and leaf appearance rate should not have been greatly affected by the artificial conditions. Contrasting growth strategies in grasses of high LAR and short leaves or low LAR and long leaves have been described for temperate grasses (Robson *et al.*, 1988), but for the three cultivars of *P. maximum* studied, only modest differences in leaf growth strategy were detected, with cv. Mombaça having longer leaves (Fig. 3) and phyllochron (Fig. 1b and 1c) and possibly a higher LER (Table 1) than cv. Tanzânia. Cv. Aruana did exhibit extensive internode elongation from an early stage of development, and in this sense behaved differently from the other two cultivars. Tiller death following defoliation (data not presented) and maintenance of a high tiller population density do seem to be issues in *P. maximum.* The data presented here show that high LER and rapid LAR observed in E1, probably due to higher temperatures in that experiment, are accompanied by lower site filling. This suggests that management strategies designed to increase the tiller population density to compensate for deaths following defoliation should focus around opportunities for manipulation of the crop during the cool season, when tillering potential is higher.

Conclusions

The rate of leaf elongation and the pattern of leaf turnover at the single tiller level was measured and the greatest effects seen in this study were differences in response between the two experiments. These differences included increased LER and LAR, and decreased number of green leaves per tiller and site filling in E1 compared with E2. These were most likely explained by warmer temperature in E1. Differences in growth strategy attributable to cultivar or defoliation height were smaller than response differences between experiments. This indicates that management strategies seeking to exploit seasonal growth patterns should offer greater scope for changing plant performance than management strategies aimed at exploiting behavioural responses of different cultivars.

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