

Herbage production and grazing losses in *Panicum maximum* cv. Mombaça under four grazing managements

R.A. CARNEVALLI¹, S.C. DA SILVA¹,
A.A.O. BUENO¹, M.C. UEBELE¹,
F.O. BUENO², J. HODGSON³, G.N. SILVA² AND
J.P.G. MORAIS²

¹ University of São Paulo — E.S.A. “Luiz de
Queiroz”, Brazil

² Federal University of São Carlos, Brazil

³ Massey University, New Zealand

Abstract

Grazing management is a key element determining herbage production and grazing efficiency. This study measured herbage accumulation and grazing efficiency in Mombaça grass pastures (*Panicum maximum* cv. Mombaça) subjected to intermittent defoliation managements. Treatments were combinations of 2 rest periods (grazing at either 95 or 100% canopy light interception — LI) and 2 grazing intensities (30 and 50 cm post-grazing height), and were allocated to 2000 m² plots according to a complete randomised block design, in a 2 × 2 factorial arrangement, with 4 replications. Response variables measured from January 2001 to February 2002 were: sward height, herbage mass and morphological composition pre- and post-grazing, and losses due to grazing. Effective values for the 95 and 100% LI targets were 95.5 and 98.5%, respectively, and corresponded with 90 and 115 cm sward height, throughout the experiment, indicating that this could be a satisfactory parameter for monitoring grazing on farms. The apparently small difference in pre-grazing targets was large enough to cause changes in dry matter accumulation and composition of the herbage mass. The 95/30 treatment resulted in lowest pre-grazing herbage mass, shortest rest period (22–24 days in spring–summer and 95 days in autumn–winter) but highest total herbage accumulation (26 890 ± s.e.m. 2506 kg/ha DM). It also

resulted in high proportion of live leaf (71%) and low proportion of live stem (15%) pre-grazing. Averaged over the 30 and 50 cm treatments, there was no difference in total herbage accumulation (22 780 ± 1772 kg/ha DM) and total herbage disappearance (20 160 ± 1170 kg/ha DM) for the LI treatments. However, grazing losses were higher for the 100% (5860 ± 550 kg/ha DM) than 95% LI treatments (4060 ± 550 kg/ha DM). Consequently, the amount of herbage effectively harvested and grazing efficiency were higher for the 95% than 100% LI treatments. The 95/30 treatment resulted in highest total herbage accumulation (26 890 ± 2506 kg/ha DM) and grazing efficiency (87%).

Introduction

Mombaça grass is a *Panicum maximum* cultivar capable of producing high levels of good quality herbage (Jank 1994; Corsi and Santos 1995). However, in order to convert that potential into production, it is necessary to understand plant morpho-physiological and ecological aspects that determine herbage production and animal performance from pastures. Recent studies have described aspects of the ecophysiology of this species (Barbosa *et al.* 1996; Machado *et al.* 1997; Santos 1997; Herling *et al.* 1998; Santos *et al.* 1999; Carvalho *et al.* 2001). In general, the results indicate high rates of herbage accumulation (Contato *et al.* 2003), particularly in summer and during reproductive development in autumn, normally associated with a considerable increase in post-grazing herbage mass and height in successive grazings (Herling *et al.* 1998). Leaf elongation rates vary according to rest periods used and measured senescence rates are usually high (Santos 1997). The accumulation of large quantities of stem and dead material demands an increase in animal selectivity for leaves in order to sustain performance, resulting in a considerable reduction in grazing efficiency as a consequence of increased losses attributed to herbage damaged

by the grazing cattle (Herling *et al.* 1998). Rest periods normally used range from 28 to 48 days (Santos 1997), 35 days being the most studied (Barbosa *et al.* 1996; Machado *et al.* 1997; Herling *et al.* 1998). The existing grazing management recommendations seem to work well only under specific circumstances and, in those conditions, the results are usually associated with low efficiency of herbage production and utilisation. Probably, this is a consequence of the conceptual base underlying the planning and conduct of experiments with tropical forage species, characterised by control of experimental conditions (treatments) through variables like stocking rate, interval between cuttings or grazings, and herbage allowance, assuming fixed values defined *a priori* regardless of available growth conditions for plants in a specific environment. These variables certainly provide means for controlling grazing management, but are not related to biological processes like plant growth and development and herbage intake by grazing animals. As a result, stocking rate and rest period (cutting or grazing) should not be considered as the primary determinants of either herbage production or animal performance. Their influence is secondary and exerted through the effect they have on a range of sward characteristics that collectively define sward structure, which in turn influence plant and animal performance.

According to Hodgson (1985), proper understanding of the effects that variations in sward structure have on plant and animal performance and on their sensitivity to grazing management practices can be achieved only in studies based on control and manipulation of specific characteristics of the sward either under steady-state conditions (*e.g.* continuous stocking) or following a pre-defined, consistent pattern of variation (*e.g.* specific targets of pre- and post-grazing conditions in rotational grazing). In this context, variables like stocking rate, herbage allowance and rest period are considered as means of achieving sward control and not as ends in themselves (Hodgson and Da Silva 2002; Da Silva 2004).

Against this background, the objective of this study was to evaluate herbage accumulation and grazing efficiency in Mombaça grass swards subjected to rotational grazing managements defined by strict control of pre- and post-grazing sward conditions: having 95 and 100% light interception (LI) by the canopy pre-grazing; and leaving 30 and 50 cm residues post-grazing.

Materials and methods

The experiment was carried out at Federal University of São Carlos, Campus Araras, Araras, SP (22°18'S, 47°23'W; 611 m asl) on a *Panicum maximum* cv. Mombaça pasture established in 1998 on a medium fertility Hapludult (Soil Survey Staff 1996). Paddocks (around 2000 m²) were grouped into 4 homogeneous blocks of 4 paddocks based on soil phosphorus (5–9 mg/dm³ in Blocks 1, 3 and 4; and 13–19 mg/dm³ in Block 2; ion-exchange resin extraction method — Raij *et al.* 1986) and base saturation levels (45–57% in Block 1; 60–70% in Block 2; 51–67% in Block 3; and 65–74% in Block 4). The experiment started on January 8, 2001 and finished on February 23, 2002, a total of 411 days.

Experimental treatments comprised combinations between 2 pre- and 2 post-grazing conditions of a rotational grazing management. Pre-grazing conditions were defined by light interception levels of the sward canopy (95 and 100%) and post-grazing conditions by residual sward heights (30 and 50 cm). These were allocated to experimental units according to a complete randomised block design, in a 2 × 2 factorial arrangement with 4 replications.

During a pre-experimental preparatory phase, paddocks were grazed intermittently to a post-grazing residue of 30 cm every 30 days from September 2000. The post-grazing residues of 30 and 50 cm were created in December, after a 2-month period of common grazing, but still using a 30-day rotation. In January 2001, after grazing to the target post-grazing heights and mowing some areas within some paddocks to ensure that the target residues had been created precisely, pre-grazing conditions started to be controlled and measurements were initiated.

Sward light interception was monitored using a canopy analyser LAI 2000 (LI-COR, Lincoln, Nebraska, USA), and measurements were performed pre- and post-grazing and at every 20-cm increase in sward height from the post-grazing condition (30 or 50 cm). When light interception by the canopy reached 90%, measurements were performed every 2 days until targets of sward pre-grazing conditions were achieved (95 and 100% LI). Readings were taken from 6 sampling areas per paddock, representative of the sward condition at the time of sampling. In each sampling area, 1 reading was taken above the canopy and 5 at ground level, totalling 6 readings above the canopy and 30 at ground level per experimental unit.

A total of 195 kg/ha of nitrogen was applied using a 20:2:17 formula (N:P:K). However, due to the variable length of the grazing cycles for individual paddocks, a consequence of the way treatments were defined, different quantities of fertiliser were used in each application in order to allow for a relatively constant amount of fertiliser being used per paddock every 2 months. Fertiliser was used from October to April, the period of reliable rainfall and high temperatures (mid-spring, summer and early autumn).

Grazing was carried out with groups of 35 lactating Holstein dairy cows, but no measurements of animal performance were made. Animals were simply used as grazers and maximum grazing time in any paddock (period of occupation) was 2 days. When necessary, a group of dry cows and heifers was used to finish the grazing session. Sward height was monitored using 2-m rulers graduated in centimetres through systematic readings along transect lines (16 points of measurement) in each paddock. Readings of sward height were taken from ground level considering the "leaf horizon" on the top of the sward as reference, even at times of the year when plants were reproductive and produced taller flowering stems.

Herbage mass was determined from herbage cuts within three 1.47×0.68 m (1 m^2) frames per plot pre- and post-grazing (adapted from Herling *et al.* 1998), allocated in areas that were representative of the average sward condition (visual assessment of height and herbage mass) at the time of sampling. Cuts were made at 20 cm from ground level in order not to damage the plant stand and future sampling procedures, given the tall-tufted growing habit of the grass species.

After cutting, samples were weighed fresh and sub-sampled, with sub-samples also weighed fresh. These were hand-dissected into live leaf (leaf lamina), live stem (leaf sheath + stem) and dead material. Weeds comprised less than 3% of the samples, so swards were considered as pure *Mombaça* grass stands. Each component was dried separately in a forced-draught oven at 65°C for 48 h and then weighed. Herbage dry matter content and its morphological composition were calculated from the results of dry weight for the sub-samples and their components, and sward herbage mass calculated accordingly. Herbage accumulation was calculated as the difference between pre-grazing and previous post-grazing herbage mass.

Litter losses to the soil pathway were quantified using three 1.5×2.0 m (3.0 m^2) frames

in each experimental unit. At the time of pre-grazing measurements, frames were allocated in areas representative of average sward condition (visual assessment of height and herbage mass) and all surface litter (un-rooted live and dead plant material on the ground) removed, leaving a clean soil surface. After grazing, these areas were re-visited and all material lying on the ground as well as broken stems and green leaves still attached and hanging on tussocks were collected. This was considered as herbage lost to litter. These samples were also sub-sampled and hand-dissected into morphological components as already described for herbage mass samples. Samples and sub-samples were dried in a forced-draught oven at 65°C for 48 h before weighing. Other losses during regrowth related to senescence were measured in a simultaneous experiment but are reported elsewhere (Carnevali *et al.* 2003).

Herbage disappearance during grazing was calculated as the difference between pre- and post-grazing herbage mass at every grazing, and the total for the experiment as the sum of the corresponding values for every grazing cycle. Harvested herbage was calculated as the difference between total herbage disappearance during grazing and that lost to litter. Litter loss was then expressed as a proportion (%) of total herbage disappearance, and its complement to 100 was considered as grazing efficiency.

As a result of the way treatments were defined, grazing dates and rest periods for each experimental unit were variable, so data were grouped according to seasons of the year for uniformity (spring = September–December; summer = January–March; and autumn–winter = April–August), and values for individual plots were weighted for the duration of records within seasons. Data were subjected to analysis of variance using the Mixed Procedure of the statistical software SAS (SAS Institute 1989) and, when appropriate, means compared by LSMeans considering a 5% significance level. The data for total dry matter accumulation and losses due to grazing for the experiment were analysed using the GLM Procedure of SAS.

Results

Number of grazings and rest periods

The number of grazings throughout the experiment was not affected by post-grazing residue but was higher for 95% LI (7.6) than for 100% LI (5.9) (Table 1), and was higher in summer (2.8)

than in spring (2.0) and autumn–winter (2.0). Consequently, average rest period varied with LI treatments and season of the year (Figure 1). The 95% LI treatments resulted in shorter rest periods (22–25 days) than the 100% LI treatments (31–40 days) during the rainy season (spring and summer). During autumn–winter, the height of post-grazing residue affected rest period, with shorter periods for the 30 cm (95–115 days) than the 50 cm treatments (140–186 days). The difference in pre-grazing condition (95 vs 100% LI) had a significant effect on sward structure (height, herbage mass and morphological composition) (Tables 2, 3, 5, 6 and 7) and affected reproductive development and flowering in late summer–early autumn.

Table 1. Total number of grazings in Mombaça grass swards subjected to rotational grazing managements from January 2001 to February 2002 (n = 4 for individual treatments; and n = 8 for main effects).

Residue (cm)	Sward light interception		
	95%	100%	Mean
30	7.0 (0.69) ¹	6.0 (0.69)	6.5 (0.49)
50	8.3 (0.69)	5.8 (0.69)	7.0 (0.49)
Mean	7.6 A ² (0.49)	5.9 B (0.49)	6.7

¹ Numbers in parentheses correspond to standard error of the mean.

² Means for sward light interception followed by the same upper case letters are not different (P>0.05).

Sward characteristics pre-grazing

Sward height was affected only by grazing frequency (95 or 100% LI) (P<0.0001). The difference between the 95 and the 100% LI treatments (90 and 115 cm, respectively) was not affected by post-grazing height (P = 0.0617), and remained relatively constant throughout the experimental period. Actual values for sward canopy light interception pre-grazing were consistent during the experiment (95.5 and 98.5% for the 95 and 100% LI treatments, respectively).

Herbage mass pre-grazing varied from 4300 to 8900 kg/ha DM for the range of treatments (Table 2), with lowest values recorded for the 95/30 treatment (4300–4800 kg/ha DM). Values for individual treatments varied with time of the year (P = 0.0026), but were relatively uniform for the 95% LI treatments. On the other hand, herbage mass was higher for the 50 cm than for the 30 cm treatments (P = 0.0016), with a difference of around 500–800 kg/ha DM during spring–summer and 2300 kg/ha DM during autumn–winter. The difference between the 50 and 30 cm residues was greater for the 95% than for the 100% LI pre-grazing condition in summer (1390 vs 240 kg/ha DM) and spring (1230 vs –230 kg/ha DM), probably a consequence of the larger increase in stem elongation and senescence rates when increasing post-grazing residue from 30 to 50 cm under the more frequent grazing management (95% LI) (Carnevalli 2003).

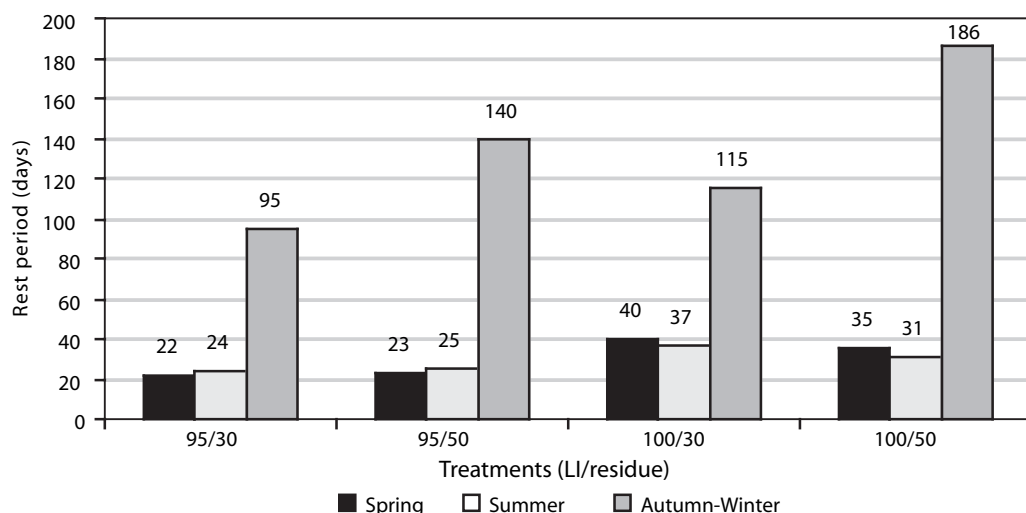


Figure 1. Average rest period for Mombaça grass swards subjected to rotational grazing managements involving pre-grazing light interception (LI) by the canopy of 95 and 100% and post-grazing residues of 30 and 50 cm from January 2001 to February 2002.

Table 2. Pre-grazing herbage mass of Mombaça grass swards subjected to rotational grazing managements from January 2001 to February 2002.

Residue (cm)	Sward light interception		
	95%	100%	Mean
	Summer (kg/ha DM)		
30	4800 C ¹ (350) ²	7220 A (350)	6010 b ⁴ (248)
50	6190 B (350)	7460 A (350)	6820 a (248)
Mean	5500 y ³ (248)	7340 x (248)	6420 Y ⁵ (175)
	Autumn–Winter (kg/ha DM)		
30	4300 C (350)	6070 B (350)	5190 b (248)
50	6320 B (350)	8630 A (350)	7480 a (248)
Mean	5310 y (248)	7350 x (248)	6330 Y (175)
	Spring (kg/ha DM)		
30	4640 C (350)	8920 A (350)	6780 a (248)
50	5870 B (350)	8690 A (350)	7280 a (248)
Mean	5260 y (248)	8800 x (248)	7030 X (175)

¹ Treatment means followed by the same upper case letter (A, B, C) within seasons are not different (P>0.05).

² Numbers in parentheses correspond to standard error of the mean.

³ Means for sward light interception within seasons followed by the same lower case letter (x, y) are not different (P>0.05).

⁴ Means for post-grazing residue within seasons followed by the same lower case letter (a, b) are not different (P>0.05).

⁵ Means for season of the year followed by the same upper case letter (X, Y) are not different (P>0.05).

In general, the 95/30 treatment resulted in a high proportion of leaf (70.9%) and a low proportion of stem (14.7%) with dead material being similar to that for other treatments (around 18.0%) (Table 3). The 100/30 treatment showed a high proportion of stem (26.4%), while morphological composition of the herbage mass for other treatments was relatively constant and around 60% leaf, 20% stem and 20% dead material. The proportion of leaf (Table 4) was highest during the rainy season (spring and summer), with the proportion of stem decreasing from summer (28.1%) and autumn–winter (28.4%) to spring (15%). The highest proportion of dead material was recorded in spring (22.7%).

Sward characteristics post-grazing

Post-grazing heights were 33.9 cm for the 95/30 and 50.1 cm for the 95/50 treatment but, for the 100% LI treatments, post-grazing heights increased for the 30 cm compared with the 50 cm residues as the experiment progressed from

summer to winter (average values of 41.7 and 53.9 cm, respectively; Table 5). This was possibly a consequence of the increasing amount of stem and dead material at the bottom of the sward. The amount of light intercepted by the canopy after grazing varied little throughout the year for the 30 and 50 cm treatments, with values around 60 and 75%, respectively, regardless of sward condition pre-grazing (95 or 100% LI). Greater post-grazing heights were associated with higher values for herbage mass (Table 6). Lowest post-grazing herbage mass was recorded for the 95/30 treatment (1500–2000 kg/ha DM) and highest for the 100/50 treatment (4500–5400 kg/ha DM).

Table 3. Morphological composition of the pre-grazing herbage mass of Mombaça grass swards subjected to rotational grazing managements.

Residue (cm)	Sward light interception		
	95%	100%	Mean
	Live leaf lamina (%)		
30	70.9 (3.11)	60.3 (3.11)	65.6 a ¹ (2.20) ²
50	57.7 (3.11)	57.5 (3.11)	57.6 b (2.20)
Mean	64.3 (2.20)	58.9 (2.20)	61.6
	Live stem (%)		
30	14.7 (2.47)	26.4 (2.47)	20.6 (1.70)
50	18.9 (2.47)	22.1 (2.47)	20.5 (1.70)
Mean	16.8 B ³ (1.75)	24.2 A (1.75)	20.5

¹ Means for post-grazing residue followed by the same lower case letter are not different (P>0.05).

² Numbers in parentheses correspond to standard error of the mean.

³ Means for sward light interception followed by the same upper case letter are not different (P>0.05).

Table 4. Morphological composition of the pre-grazing herbage mass of Mombaça grass swards subjected to rotational grazing managements from January 2001 to February 2002.

Component	Season of the year			Mean
	Summer	Autumn–Winter	Spring	
	(%)			
Live leaf	60.6 A ¹ (0.67) ²	57.3 B (2.27)	62.9 A (2.40)	61.6
Live stem	28.1 A (2.50)	28.4 A (2.50)	15.0 B (2.50)	20.5
Dead material	14.1 B (1.74)	15.9 B (1.74)	22.7 A (1.74)	17.9

¹ Within rows, means followed by the same upper case letters are not different (P>0.05).

² Numbers in parentheses correspond to standard error of the mean.

Table 5. Post-grazing sward height of Mombaça grass subjected to grazing at 95 and 100% canopy light interception, leaving post-grazing residues of 30 and 50 cm.

Residue (cm)	Sward light interception		
	95%	100%	Mean
	(cm)		
30	33.9 D ¹ (0.81) ²	41.7 C (0.81)	37.8 b ³ (0.57)
50	50.1 B (0.81)	53.9 A (0.81)	52.0 a (0.57)
Mean	42.0 Y ⁴ (0.57)	47.8 X (0.57)	44.9

¹ Treatment means followed by the same upper case letter (A, B, C, D) are not different ($P>0.05$).

² Numbers in parentheses correspond to standard error of the mean.

³ Means for post-grazing residue followed by the same lower case letter are not different ($P>0.05$).

⁴ Means for sward light interception followed by the same upper case letter (X, Y) are not different ($P>0.05$).

Table 6. Post-grazing herbage mass (kg/ha DM) of Mombaça grass swards subjected to rotational grazing managements from January 2001 to February 2002.

Residue (cm)	Sward light interception		
	95%	100%	Mean
	Summer		
30	1470 C ¹ (166) ²	3300 B (166)	2390 b ⁴ (118)
50	3990 A (166)	4470 A (166)	4230 a (118)
Mean	2730 y ³ (118)	3890 x (118)	3310 (83)
	Autumn–Winter		
30	2010 C (346)	3030 B (346)	2520 b (244)
50	3740 B (346)	5390 A (346)	4570 a (244)
Mean	2870 y (244)	4210 x (244)	3540 (173)
	Spring		
30	1830 D (197)	2920 C (197)	2380 b (140)
50	4270 B (197)	4920 A (197)	4590 a (140)
Mean	3050 y (140)	3920 x (140)	3490 (99)

¹ Within seasons, treatment means followed by the same upper case letter are not different ($P>0.05$).

² Numbers in parentheses correspond to standard error of the mean.

³ Means for sward light interception within seasons followed by the same lower case letter (x, y) are not different ($P>0.05$).

⁴ Means for post-grazing residue within seasons followed by the same lower case letter (a, b) are not different ($P>0.05$).

The morphological composition of the post-grazing herbage mass varied with treatments and season of the year. In general, more frequent defoliations (95% LI) resulted in higher proportions of leaf (41–49%) than less frequent defoliations

(100% LI) (32–36%) throughout the year (Table 7). Leaf proportion declined in the autumn–winter period. Swards grazed down to 30 cm showed smaller proportions of stem (25.8%) than those grazed to 50 cm (30.2%). The 95% LI treatments resulted in lower proportions of stem than the 100% LI treatments (23.1 and 32.8%, respectively). Stem proportion was highest in summer (33.9%) and was comprised mainly of vegetative stems, particularly for the most lenient and less frequent grazing treatment (100/50). During autumn–winter, there was a small reduction in the proportion of stems (29.5%), but a relative increase in reproductive compared with vegetative stems. Lowest values were recorded in spring (21.5%).

Table 7. Proportion of live leaf (%) in the post-grazing herbage mass of Mombaça grass swards subjected to rotational grazing managements from January 2001 to February 2002.

Residue (cm)	Sward light interception		
	95%	100%	Mean
	Summer		
30	50.5 A ¹ (1.69) ²	31.1 C (1.69)	40.8 (1.19)
50	42.0 B (1.69)	35.4 C (1.69)	38.7 (1.19)
Mean	46.2 x ³ (1.19)	33.3 y (1.19)	39.8 XY ⁴ (0.84)
	Autumn–Winter		
30	39.5 AB (2.75)	34.2 BC (2.75)	36.8 (1.95)
50	42.7 A (2.75)	29.2 C (2.75)	35.9 (1.95)
Mean	41.1 x (1.95)	31.7 y (1.95)	36.4 Y (1.38)
	Spring		
30	48.9 A (3.06)	37.2 B (3.06)	43.0 (2.17)
50	49.0 A (3.06)	34.3 B (3.06)	41.7 (2.17)
Mean	48.9 x (2.17)	35.8 y (2.17)	42.3 X (1.53)

¹ Within seasons, treatment means followed by the same upper case letter (A, B, C) are not different ($P>0.05$).

² Numbers in parentheses correspond to standard error of the mean.

³ Means for sward light interception within seasons followed by the same lower case letter (x, y) are not different ($P>0.05$).

⁴ Means for season of the year followed by the same upper case letter (X, Y) are not different ($P>0.05$).

The proportion of dead material in the post-grazing herbage mass was higher for the 30 cm treatments (34.8%), particularly when associated with the 100% LI pre-grazing condition. The lowest proportion of dead material for the experiment was recorded during summer (25.6%), with values increasing significantly through autumn–winter (35.1%) to spring (37%).

Herbage accumulation

Grazing to 30 cm resulted in higher dry matter accumulation during the study than grazing to 50 cm ($P = 0.0348$, Table 8), while level of light interception by the canopy had no significant effect. Herbage accumulation during summer (9930 kg/ha DM) was higher than in autumn–winter and spring (5900 and 6670 kg/ha DM, respectively) (Table 9). Daily accumulation rates calculated on a monthly basis ranged from 15 to 150 kg/ha and were higher in summer (110) than in spring (75), autumn (45) and winter (25), indicating a strong seasonality of production.

Table 8. Herbage accumulation of *Mombaça* grass swards subjected to rotational grazing managements.

Residue (cm)	Sward light interception		
	95%	100%	Mean
	(kg/ha DM)		
30	26 890 (2 506)	24 890 (2 506)	25 890 a ¹ (1 772) ²
50	18 520 (2 506)	20 820 (2 506)	19 670 b (1 772)
Mean	22 710 (1 772)	22 860 (1 772)	22 780

¹ Means for post-grazing residue followed by the same lower case letter are not different ($P > 0.05$).

² Numbers in parentheses correspond to standard error of the mean.

Table 9. Herbage accumulation of *Mombaça* grass swards subjected to rotational grazing managements from January 2001 to February 2002.

Sward light interception (%)	Season of the year			Total
	Summer	Autumn–Winter	Spring	
	(kg/ha DM)			
95	10 680 (779)	5 250 (779)	6 480 (779)	22 410 (1 764)
100	9 180 (779)	6 550 (779)	6 860 (779)	22 590 (1 764)
Mean	9 930 A ¹ (550) ²	5 900 B (550)	6 670 B (550)	22 500

¹ Means for season of the year followed by the same upper case letter are not different ($P > 0.05$).

² Numbers in parentheses correspond to standard error of the mean.

Herbage disappearance and litter losses

Dry matter disappearance on the 30 cm treatments was 5630 kg/ha DM greater than on the 50 cm treatments during grazing (Table 10), and more disappeared in summer than in autumn–winter and spring (9970, 4470 and 5720 kg/ha DM, respectively). The proportion of the total

herbage, which disappeared during grazing, was similar for the 30 and 50 cm treatments (85 and 86%, respectively) and also for the 95 and 100% LI treatments (89 and 91%).

Table 10. Herbage disappearance in *Mombaça* grass swards subjected to rotational grazing managements with residues of 30 and 50 cm from January 2001 to February 2002.

Residue (cm)	Season of the year			Total
	Summer	Autumn–Winter	Spring	
	(kg/ha DM)			
30	11 540 (1 411)	4 800 (779)	6 130 (770)	22 470 a ¹ (1 170) ²
50	8 390 (1 411)	4 140 (779)	4 310 (770)	16 840 b (1 170)
Mean	9 970 A (521)	4 470 B (521)	5 720 B (521)	

¹ Means for post-grazing residue followed by the same lower case letter are not different ($P > 0.05$).

² Numbers in parentheses correspond to standard error of the mean.

³ Means for season of the year followed by the same upper case letter are not different ($P > 0.05$).

Litter losses were lower for the 95% than the 100% LI treatments (4060 vs 5860 kg/ha DM; Table 11). By deduction, the amount of herbage apparently harvested during grazing was 15 810 and 14 600 kg/ha DM for the 95 and 100% LI treatments, equivalent to grazing efficiencies of around 79 and 71%, respectively.

For the 30 and 50 cm treatments, litter losses were 4470 and 5450 kg/ha DM, resulting in 18 000 and 11 390 kg/ha DM being harvested and grazing efficiencies of around 80 and 68%, respectively. The combination of short rest period (95% LI) and hard grazing (30 cm residue) resulted in the lowest values of litter loss being recorded during summer (Table 11).

The morphological composition of the herbage lost to litter varied with treatment (Tables 12, 13 and 14). On the 100% LI treatments, losses contained higher proportions of stem than on the 95% LI treatments (Table 12). The proportion of stem (around 12%) was not affected by season of the year for the 95% LI but, for the 100% LI treatments, the proportion of stem varied from 20.4% in summer to 14.5% in autumn–winter and 10.7% in spring. The proportions of leaf were higher for the 95/30 and 100/50 than for the 100/30 treatment, with the 95/50 treatment in an intermediate position (Table 13). Values recorded in summer (37.1%) were higher than in autumn–winter (25.7%) and spring (27.2%). Dead material was the main component of the herbage lost during

grazing (57%), with the highest proportion in the 95/50 treatment (61.6%) (Table 14).

Table 11. Litter losses (kg/ha DM) during grazing of Mombaça grass swards subjected to rotational grazing managements from January 2001 to February 2002.

Residue (cm)	Sward light interception			Mean
	95%	100%		
	Summer			
30	1050 B ¹ (444) ²	3420 A (444)		2230 (314)
50	2810 A (444)	2860 A (444)		2840 (314)
Mean	1930 y ³ (314)	3140 x (314)		2530 X ⁴ (222)
	Autumn–Winter			
30	640 A (444)	1530 A (444)		1090 (314)
50	710 A (444)	710 A (444)		710 (314)
Mean	680 x (314)	1120 x (314)		900 Z (222)
	Spring			
30	1430 AB (444)	860 B (444)		1150 (314)
50	1480 AB (444)	2330 A (444)		1910 (314)
Mean	1460 x (314)	1600 x (314)		1530 Y (222)
	Total			
30	3120 B (778)	5810 A (778)		4470 (550)
50	5000 AB (778)	5900 A (778)		5450 (550)
Mean	4060 y (550)	5860 x (550)		4960

¹ Treatment means followed by the same upper case letter within seasons (A, B) are not different (P>0.05).

² Numbers in parentheses correspond to standard error of the mean.

³ Means for sward light interception within seasons followed by the same lower case letter (x, y) are not different (P>0.05).

⁴ Means for season of the year followed by the same upper case letter (X, Y, Z) are not different (P>0.05).

Table 12. Proportion of live stems in the litter loss during grazing of Mombaça grass swards subjected to rotational grazing at either 95 or 100% canopy sward light interception from January 2001 to February 2002.

Sward light interception (%)	Season of the year			Mean
	Summer	Autumn–Winter	Spring	
	(%)			
95	13.1 Ab ¹ (1.75) ²	11.2 Aa (1.75)	10.9 Aa (1.75)	11.7 b (0.93)
100	20.4 Aa (1.75)	14.5 Ba (1.75)	10.7 Ba (1.75)	15.2 a (0.93)
Mean	16.7 A (1.24)	12.9 B (1.24)	10.8 B (1.24)	13.5

¹ Means followed by the same lower case letter in columns and upper case letter in rows are not different (P>0.05).

² Numbers in parentheses correspond to standard error of the mean.

Table 13. Proportion of live leaf in the litter loss during grazing of Mombaça grass swards subjected to rotational grazing managements.

Residue (cm)	Sward light interception			Mean
	95%	100%		
	(%)			
30	31.6 A ¹ (1.76) ²	24.7 C (1.76)		28.1 (1.24)
50	25.7 BC (1.76)	31.0 AB (1.76)		28.3 (1.24)
Mean	28.6 (1.24)	27.8 (1.24)		28.2

¹ Treatment means followed by the same upper case letter are not different (P>0.05).

² Numbers in parentheses correspond to standard error of the mean.

Table 14. Proportion of dead material in the litter loss during grazing of Mombaça grass swards subjected to rotational grazing managements.

Residue (cm)	Sward light interception			Mean
	95%	100%		
	(%)			
30	55.7 AB ¹ (2.97) ²	59.9 AB (2.97)		57.8 (2.10)
50	61.6 A (2.97)	50.5 B (2.97)		56.1 (2.10)
Mean	58.7 (2.10)	55.2 (2.10)		57.0

¹ Treatment means followed by the same upper case letter are not different (P>0.05).

² Numbers in parentheses correspond to standard error of the mean.

Discussion

The grazing process was monitored carefully to ensure that sward targets for both pre- and post-grazing conditions were adequately maintained. Actual values of canopy light interception pre-grazing were very close to planned targets (95.5 and 98.5% for the 95 and 100% LI treatments, respectively). The 100% LI target could not be reached, even when equipment was used under complete darkness (maximum reading of 99%). On the other hand, the 30 and 50 cm post-grazing residue targets were maintained only with the 95% LI pre-grazing condition. Less frequent grazing (100% LI) allowed accumulation of stems and dead material, increasing the difficulty in grazing swards down to planned residues, particularly 30 cm.

Pre-grazing sward height was consistent throughout the experiment, with values around 90 and 115 cm for the 95 and 100% LI treatments, respectively, regardless of time of the year and

physiological state of plants (vegetative or reproductive). Similar results were reported by Barbosa (2004) for Tanzânia grass (*Panicum maximum* cv. Tanzânia) where 95 and 100% LI corresponded with sward surface heights of 70 and 85 cm, respectively. These results indicate that sward height could be used as a practical field guide to monitor and manage the grazing process.

Pre-grazing herbage mass also showed limited variation throughout the year (Table 2). However, its use as a field guide to monitor grazing is not as practical as sward height, since measurements are not as simple and/or require observers with very accurate visual appraisal skills. More frequent grazing (95% LI treatments) resulted in lower pre-grazing herbage mass than less frequent grazing (100% LI treatments). Similar results were reported by Santos *et al.* (1999) and Barbosa (2004) for rotationally grazed Mombaça and Tanzânia grass, respectively. Despite the lower pre-grazing herbage mass at 95% LI, the number of grazing cycles was higher (Table 1), resulting in similar total herbage accumulation on the 95 and 100% LI treatments over the course of the experiment (Table 8). This indicates that longer rest periods would not necessarily result in higher herbage accumulation and that, in fact, herbage produced under those circumstances would certainly have a lower nutritive value, a result of the high proportions of stem and dead material at the time of grazing. Measurements of growth and senescence throughout every regrowth cycle during the experiment showed a steady decline in leaf elongation and a steady increase in stem elongation and senescence rates from the beginning towards the end of regrowth (Carnevali 2003). This behaviour was more pronounced when comparing 50 vs 30 cm residues for 95% LI and 95 vs 100% LI across post-grazing residues, and would explain the larger differences in pre-grazing herbage mass between the 50 and 30 cm residues for the 95% LI when compared with the 100% LI treatments (Table 2).

Overall, around 23 tonnes of dry matter were produced per hectare using no irrigation and only 195 kg/ha N, with post-grazing residue being the main determinant of herbage accumulation. Despite no statistical significance, treatment 95/30 accumulated 26 890 kg/ha DM, equivalent to 8370 and 6070 kg/ha DM more than the 95/50 and 100/50 treatments, respectively. These differences are large in agronomic and biological terms and should not be disregarded. There was

a strong seasonal variation in herbage production (Table 9), suggesting that efficient grazing management practices would have to be associated with strategic use of forage conservation and supplementation practices. Greatest herbage accumulation rates occurred during summer, the time of year with favourable climatic conditions for pasture growth. During autumn–winter, rest periods were shorter for 30 cm than for 50 cm residues, a likely consequence of better control of reproductive development and flowering that allowed plants to continue producing and elongating leaves.

The increase of only 3–4 units in target LI% by the sward pre-grazing increased the average rest period from 23 days to 38 days in spring–summer and this resulted in a significant change in sward structure. Morphological composition of the herbage pre-grazing varied, with the proportion of stem being lower for the 95% than the 100% LI treatments (Table 3). Additionally, swards grazed down to 50 cm residue had lower proportion of leaf pre-grazing, suggesting that less frequent (100% LI) and more lenient (50 cm) grazing management practices could result in deterioration of sward structure by the accumulation of stem and dead material and also reduce the nutritive value of the herbage on offer (Bueno 2003). Most *Panicum* pastures in Brazil are commonly managed using rest periods of 28–48 days (Santos 1997) and post-grazing residues of 50–60 cm, conditions that are similar to the 100% LI treatments in this experiment.

Several experiments with *Panicum maximum* under grazing have revealed similar patterns of response in sward morphological components with variations in grazing management. Santos *et al.* (1999) reported high accumulation of stem material in Tanzânia grass subjected to rotational grazing managements characterised by fixed rest periods of 28, 38 and 48 days. Gomes (2001), studying daily herbage allowance (4, 8 and 12 kg DM/100 kg LW/day) and duration of the period of occupation (1 and 3 days) in Mombaça grass under rotational grazing, reported a progressive increase in post-grazing sward height caused by the increasing difficulty in the grazing-down process associated with increasing quantities and proportions of stem in the residual herbage mass. Pinto *et al.* (1994), working with Guinea grass (*Panicum maximum* cv. Guinea), reported decreasing values for leaf:stem ratio (1.3, 1.2, 1.0, 0.7 and 0.5) with increasing rest periods

(14, 28, 42, 56 and 70 days, respectively). Cândido *et al.* (2003), studying morphogenetic traits of Mombaça grass subjected to rotational grazing characterised by defoliation intervals defined as the time necessary for the appearance of 2.5, 3.5 and 4.5 fully expanded leaves per tiller, indicated that stem elongation and accumulation were reduced (controlled) with more frequent grazing. In all these experiments, there was an intense development and accumulation of stems associated with long rest periods. In the present study, control of stem growth was effective only in the 95/30 treatment, indicating that long rest periods for grass species characterised by a tall, erect growth habit, *e.g. Panicum*, would inevitably make it difficult to control sward structure and most likely limit leaf growth and grazing efficiency in subsequent regrowth periods (Carnevalli 2003).

The proportion of leaf in the post-grazing residue varied from 40 to 50% and from 29 to 37% for the 95 and 100% LI treatments, respectively. These values can be considered high and are probably a consequence of the cutting height used to harvest samples (20 cm) that did not take into account the material positioned closer to ground level, certainly comprised almost exclusively of stems and dead material. This would impair comparison of the results from this experiment with others available in the literature and recorded from cuts taken to ground level. The difference of only 10–20 percentage units in the proportion of leaf among treatments may be a consequence of the reduced stem elongation under more frequent grazing, favouring a higher proportion of leaf in the residue. Teixeira (1998) reported 16% leaf in the post-grazing herbage mass of Tobiã grass (a *Panicum maximum* cultivar) subjected to a 33-day rotational grazing regimen.

Grazing resulted in a reduction of around 20 percentage units in the proportion of leaves (Tables 3 and 7) and an increase of 8–10 percentage units in the proportion of stems and dead material in the post- compared with the pre-grazing herbage mass. Brâncio *et al.* (2000), using *Panicum maximum* cultivars, also reported an increase in stem and dead material and a reduction in leaf proportion in the herbage post-grazing compared with the herbage pre-grazing, and associated the results with selective harvest of leaves by the grazing animals. Teixeira (1998) reported the same pattern of response for Tobiã grass under a 33-day rotational grazing management.

Part of the pool of herbage, which disappeared during grazing (Table 10), was lost as a consequence of physical damage and/or rejection, with no difference in total litter loss between the 30 and 50 cm treatments (Table 11). Litter losses were greater in spring than in autumn–winter for all treatments except the 100/30, probably because it took longer for paddocks subjected to that treatment to reach pre-grazing targets in spring (longer grazing cycles) and, as a consequence, the number of grazings was smaller. A smaller number of grazings would correspond with less physical damage and/or rejection and, as a result, a smaller amount of herbage being lost. Since the 30 cm treatments accumulated more herbage than the 50 cm treatments, they had a much higher grazing efficiency (80%) than the 50 cm treatments (68%), particularly the 95/30 treatment. In general, the 95% LI treatments resulted in 30% (1800 kg/ha) less litter loss during grazing than the 100% LI treatments (Table 11). Considering that grazing efficiency for the 95 and 100% LI treatments was 79 and 71%, respectively, it might be inferred that higher grazing efficiency could be related to the higher proportion of leaves and lower proportion of stem in the more frequently grazed swards (Table 3), particularly the 95/30 treatment, since stems are a deterrent to grazing and can reduce grazing efficiency. Gonçalves (2002) also reported higher grazing efficiency for more frequently defoliated Marandu grass swards (*Brachiaria brizantha* cv. Marandu). Quadros *et al.* (2001) found that increasing N-fertiliser rates increased herbage losses (equivalent to litter losses in this paper) in Mombaça and Tanzânia pastures when no adjustment (reduction) was made in rest period to compensate for the higher herbage accumulation rates, which resulted. These findings indicate that grazing frequency is a powerful tool to control sward structure and can improve grazing efficiency.

Proper understanding of the grazing process requires not only quantification of the herbage being lost but also knowledge of the composition of the lost herbage. Litter losses for the 100% LI showed a higher proportion of stem than for the 95% LI treatments (Table 12), most likely a consequence of the higher accumulation of stem material under those circumstances. The 100/50 treatment resulted in a high proportion of leaf in the litter loss (Table 13), probably because of trampling observed, particularly for that grazing management strategy. Under those

conditions, pre-grazing herbage mass was consistently higher and, when animals were allowed into the paddocks, physical contact and trampling were greater than in other treatments with lower pre-grazing herbage masses. Another indicator that losses in this treatment were not exclusively related to selective grazing was the low proportion of dead material in the litter (Table 14), since all swards had around 18% of this plant component at pre-grazing. The 95/30 treatment also showed a high proportion of leaf in the litter loss, but it also had a high proportion of leaf in the pre-grazing herbage mass.

Conclusions

Grazing management practices based on principles of plant ecophysiology take into account the potential for growth of pastures in different environments and allow for the definition of site-specific recommendations, a basic requirement for generalisation and planning of flexible and efficient grazing management practices. In that sense, sward height is a reliable, practical parameter for use as a field guide or reference for monitoring and managing the grazing process.

High dry matter accumulation and grazing efficiency are achieved with 90 cm pre- (95% LI) and 30 cm post-grazing sward height targets, respectively, a more frequent and intense defoliation grazing management than traditionally used. Longer rest periods (*e.g.* 100% LI treatments) do not necessarily ensure higher dry matter accumulation, and nutritive value of the harvested herbage may be reduced because of more stem and dead material relative to leaf, a condition that would certainly impair animal performance and productivity. Similar experiments with *Panicum maximum* (cvv. Tanzânia, Tobiata, Massai and Atlas) and *Brachiaria brizantha* cv. Marandu showed that the general relationship between sward height, light interception and herbage accumulation was consistent, but sward height at which 95% LI was achieved was specific for each grass species.

Adoption of a sward target-based grazing management would involve adjusting stocking rate according to herbage accumulation rates at different times of the year. During spring and summer, areas might have to be set aside for fodder conservation for feeding back during winter when herbage accumulation rates are lower. This would be especially so for the more

intensive dairying and beef fattening systems usually characterised by high nitrogen fertiliser inputs and irrigation, clearly indicating the need to change paradigms and re-think research protocols in order to accomplish such goals.

Acknowledgements

Thanks are due to: Professor Domicio do Nascimento Junior for valuable comments during the elaboration of this paper; FAPESP and CNPq for financial support; and the research team at USP/ESALQ, Brazil.

References

- BARBOSA, M.A.A.F., DAMASCENO, J.C., CECATO, U. and SAKAGUTI, E.S. (1996) Estudo de perfilhamento em 4 cultivares de *Panicum maximum* Jacq. submetidos a duas alturas de corte. *Proceedings of the Reunião Anual da Sociedade Brasileira de Zootecnia, Fortaleza, Brazil, 1996*. **33**, 109–111.
- BARBOSA, R.A. (2004) *Características morfofisiológicas e acúmulo de forragem em capim-tanzânia* (*Panicum maximum* Jacq. cv. Tanzânia) submetido a frequências e intensidades de pastejo. Ph.D. Thesis. Federal University of Viçosa.
- BRÂNCIO, P.A., EUCLIDES, V.P.B. and NASCIMENTO, D. Jr (2000) Avaliação de três cultivares de *Panicum maximum* Jacq. sob pastejo. 2. Proporções de folha, talo e material morto da pastagem e seletividade em pastejo. *Proceedings of the Reunião Anual da Sociedade Brasileira de Zootecnia, Viçosa, Brazil, 2000*. **37** (compact disc).
- BUENO, A.A.O. (2003) *Características estruturais do dossel forrageiro, valor nutritivo e produção de forragem em pastos de capim-Mombaça submetidos a regimes de lotação intermitente*. Masterate Degree Thesis. University of São Paulo (available at www.teses.usp.br).
- CÂNDIDO, M.J.D., ALEXANDRINO, E. and GOMIDE, J.A. (2003) Análise de crescimento em *Panicum maximum* cv. Mombaça sob condições de campo. *Proceedings of the Reunião Anual da Sociedade Brasileira de Zootecnia, Santa Maria, Brazil, 2003*. **40** (compact disc).
- CARNEVALLI, R.A. (2003) *Dinâmica da rebrotação de pastos de capim-Mombaça submetidos a regimes de desfolhação intermitente*. Ph.D. Thesis. University of São Paulo (available at www.teses.usp.br).
- CARNEVALLI, R.A., DA SILVA, S.C., BUENO, A.A.O., UEBELE, M.C., BUENO, F.O. and MORAIS, J.P. (2003) Dinâmica do acúmulo de forragem em pastos de capim Mombaça submetidos a regimes de desfolhação intermitente. *Proceedings of the Reunião Anual da Sociedade Brasileira de Zootecnia, Santa Maria, Brazil, 2003*. **40** (compact disc).
- CARVALHO, D.D., MATHEW, C. and HODGSON, J. (2001) Effect of aging in tillers of *Panicum maximum* on leaf elongation rate. *Proceedings of the XIX International Grassland Congress, São Pedro, Brazil, 2001*. **19**, 41–42.
- CONTATO, E.D., GOMIDE, C.A.M., REIS, R.A. and DE LUCA, S. (2003) Efeitos de períodos de descanso e resíduos pós-pastejo na produção e estrutura da vegetação de *Panicum maximum* cv. Tanzânia sob lotação intermitente. *Proceedings of the Reunião Anual da Sociedade Brasileira de Zootecnia, Santa Maria, Brazil, 2003*. **40** (compact disc).

- CORSI, M. and SANTOS, P.M. (1995) Potencial de produção do *Panicum maximum*. *Proceedings of the Simpósio Sobre Manejo da Pastagem, Piracicaba, Brazil, 1995*, **11**, 275–304.
- DA SILVA, S.C. (2004) Understanding the dynamics of herbage accumulation in tropical grass species: the basis for planning efficient grazing management practices. *Proceedings of Symposium on Grassland Ecophysiology and Grazing Ecology, UFPR, Curitiba, Brazil, 2004*, **2** (compact disc).
- GOMES, M.A. (2001) *Efeitos de intensidades de pastejo e períodos de ocupação da pastagem na massa de forragem e nas perdas e valor nutritivo da matéria seca do capim-mombaça (Panicum maximum Jacq. cv. Mombaça)*. Masterate Degree Thesis. University of São Paulo (available at www.teses.usp.br).
- GONÇALVES, A.C. (2002) *Características morfológicas e padrões de desfolhação em pastos de capim marandu submetidos a regimes de lotação contínua*. Masterate Degree Thesis. University of São Paulo (available at www.teses.usp.br).
- HERLING, V.R., JANTALIA, C.P., PIAZZA, C., SUDA, C.H., LUZ, P.H.C. and LIMA, C.G. (1998) Determinação da matéria seca disponível do capim Mombaça (*Panicum maximum* Jacq. cv. Mombaça) sob pastejo. *Proceedings of the Reunião Anual da Sociedade Brasileira de Zootecnia, Botucatu, Brazil, 1998*, **35**, 530–532.
- HODGSON, J. (1985) The significance of sward characteristics in the management of temperate sown pastures. *Proceedings of the XV International Grassland Congress, Kyoto, Japan, 1985*, **15**, 63–66.
- HODGSON, J. and DA SILVA, S.C. (2002) Options in tropical pasture management. *Proceedings of Reunião Anual da Sociedade Brasileira de Zootecnia, Recife, Brazil, 2002*, **39**, 180–202.
- JANK, M.B. (1994) Potencial do gênero *Panicum*. *Proceedings of the Simpósio Brasileiro de Forrageiras e Pastagens, Campinas, Brazil, 1994*, pp. 25–31.
- MACHADO, A.O., CECATO, U., MIRA, R.T., PEREIRA, L.A.F., MARTINS, E.N., DAMASCENO, J.C. and SANTOS, G.T. (1997) Avaliação de genótipos de *Panicum maximum* (Jacq) em duas alturas de corte. *Proceedings of the Reunião Anual da Sociedade Brasileira de Zootecnia, Juiz de Fora, Brazil, 1997*, **34**, 219–221.
- PINTO, J.C., GOMIDE, J.A. and MESTRI, M. (1994) Produção de matéria seca e relação folha:caule de gramíneas forrageiras tropicais, cultivadas em vasos, com duas doses de nitrogênio. *Revista da Sociedade Brasileira de Zootecnia*, **23**, 313–326.
- QUADROS, P.S., RODRIGUES, L.R.A., FAVORETTO, V., MALHEROS, E.B. and RAMOS, A.K.B. (2001) Perdas de forragem em pastagens dos cultivares tanzânia e mombaça de *P. maximum* Jacq. adubadas com 4 doses de N, P e K. *Proceedings of the Reunião Anual da Sociedade Brasileira de Zootecnia, Piracicaba, Brazil, 2001*, **38**, 294–296.
- RAIJ, B. VAN, QUAGGIO, J.A. and SILVA, N.M. (1986) Extraction of phosphorus, potassium, calcium, and magnesium from soils by ion-exchange resin procedure. *Communications in Soil Science and Plant Analysis*, **17**, 547–566.
- SANTOS, P.M. (1997) *Estudo de características de Panicum maximum (Jacq.) cvs. Tanzânia e Mombaça para estabelecer seu manejo*. Masterate Degree Thesis. University of São Paulo (available at www.teses.usp.br).
- SANTOS, P.M., CORSI, M. and BALSALOBRE, M.A.A. (1999) Efeito da frequência de pastejo e da época do ano sobre a produção e a qualidade em *Panicum maximum* cvs. Tanzânia e Mombaça. *Revista Brasileira de Zootecnia*, **28**, 244–249.
- SAS INSTITUTE (1989) *SAS/STAT™. Guide for personal computers*. Version 7. (SAS Institute Inc.: Cary, NC).
- SOIL SURVEY STAFF (1996) *Keys to soil taxonomy*. 7th Edn. (US Government Printing Office: Washington, DC).
- TEIXEIRA, E.I. (1998) *Avaliação de características morfológicas e nutricionais do capim-Tobiatã (Panicum maximum cv. Tobiatã) sob sistema de pastejo rotacionado*. Masterate Degree Thesis. University of São Paulo (available at www.teses.usp.br).

(Received for publication March 18, 2005; accepted October 3, 2005)