Scientia Agricola

Adaptation of the C_4 grass *Panicum maximum* to defoliation is related to plasticity of N uptake, mobilisation and allocation patterns

Patricia Menezes Santos[1]*, Barry Thornton[2], Moacyr Corsi[3]

[1]Embrapa Pecuária Sudeste, Rod. Washington Luiz, km 234, C.P. 339 – 13568-800 – São Carlos, SP – Brasil.
[2]The James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH – UK.
[3]USP/ESALQ – Depto. de Zootecnia, C.P. 09 – 13418-900 – Piracicaba, SP – Brasil.
*Corresponding author <patricia@cppse.embrapa.br>

Edited by: Leonardo Oliveira Medici

Received September 23, 2011
Accepted March 06, 2012

ABSTRACT: Dry mass production and persistence of *Panicum maximum* pastures depends on nitrogen supply. Defoliation influences N uptake and allocation patterns yet its effects on plasticity of N dynamics in *P. maximum* have not been investigated. Stable isotopes of N (^{15}N) were used in order to test the hypothesis that defoliation in terms of proportion of the leaf area removed effects N mobilisation, uptake and allocation patterns in *P. maximum*. The plants were initially cut weekly to a height of either 0.15 m or 0.30 m for seven weeks. Eight weeks after the first defoliation, all plants were defoliated for a final time to remove 0, 25, 50, 75 or 100 % of the area of each individual leaf blade of the main tiller. Root N uptake was reduced when all leaf area was removed, but more lenient defoliation improved N uptake due to a positive effect on specific N uptake. Young leaves, side tillers and roots were the main sinks for N from root uptake. Roots of *P. maximum* became a net source of N for mobilisation immediately after severe defoliation. Root uptake was the main source of N for new growth in *P. maximum* plants. Allocation pattern of mobilised N was different from that of N derived from root uptake. It was concluded that adaptation of *P. maximum* to defoliation is related to plasticity of N uptake, mobilisation and allocation, but changes in N dynamics did not offset negative impacts of complete defoliation of the plants.
Keywords: clipping height, guineagrass, organic reserves, regrowth, tropical grass

Introduction

P. maximum is a tropical grass originally from Africa (Muir and Jank, 2004). Commercial cultivars are recommended for regions with 800 to 1800 mm of annual rainfall in well-drained soils (Muir and Jank, 2004). In Brazil, it has been used for grazing and silage production because of its high dry mass production, but it does not sustain heavy defoliation in areas of low soil fertility.

Dry mass production and persistence of *P. maximum* pastures depend on N supply (Andrade et al, 2001). The ability of plants to store, mobilise and reuse N has been suggested as a mechanism of adaptation to lower soil fertility environments (Aldana and Berendse, 1997). Santos et al. (2002) observed that as N supply was reduced the C_3 grass *Poa trivialis* was more plastic in the allocation of mobilised N than the C_4 grass *P. maximum* and suggested this may be related to the low persistence of *P. maximum* pastures when established in areas of relative low soil fertility.

Defoliation is an additional influence on N uptake and allocation patterns in plants (see reviews by Volenec et al., 1996; Schnyder et al., 2000; Thornton et al., 2000) and its effects on plasticity of N dynamics in *P. maximum* have yet to be investigated. Predicting the response of grassland net primary production to increased grazing intensity requires a better understanding of N dynamics in the soil-plant system (Leriche et al., 2001).

Nitrogen availability for regrowth may be reduced after defoliation due to a decrease in the N pool from senescing leaves, lower root growth or a reduction in soil N flux induced by lower crop transpiration (Lestienne et al., 2006; Gastal et al., 2010; Durand et al., 2010). On the other hand, plants can adapt to defoliation intensity by changing their shoot and root morphology and growth rate (Matthew et al., 2000; Gastal et al., 2010) and, consequently, changing both the amount of shoot material and N stores bellow cutting height and the exploitation of the soil by roots for water and nutrients uptake. Increased N uptake per unit of root dry weight due to repeated defoliation has also been reported in the literature, enough to mitigate the observed reduction of root mass for some species (Thornton and Millard, 1996).

Plants may be defoliated in contrasting ways each with different consequences for the plants ability to adapt. When plants are trimmed to a specific height, both leaf and sheath material can be removed. Alternatively, defoliation may be on a leaf basis, removing a specific percentage of the area of each leaf. This approach will not damage sheaths and leaf meristems. This study aimed to investigate the effect of different defoliation treatments on the plasticity of N uptake and allocation patterns of *P. maximum*. The hypothesis that defoliation to a set cutting height and in terms of the proportion of the leaf area removed affects N mobilisation, uptake and allocation patterns in the C_4 grass *Panicum maximum* was tested. The implications of results for management practices to improve grassland persistence were also discussed.

Materials and Methods

Plant establishment

Eighty pots measuring 0.23 m in diameter were filled with course sand (1 – 10 mm diameter) to a depth of 10 mm and the remaining space was filled with fine sand (0.25 – 0.7 mm diameter). The total volume of sand used was 5.4 L. A disc of Tygan mesh (Bradley Lomas

Electrolok Ltd, Eckington, UK) covered by a single layer of Whatman No 1 filter paper at the base of the pots prevented sand loss through the drainage holes. All filled pots were completely flushed with deionised water three times. Fifteen seeds of *Panicum maximum* (Jacq.) cv. Tanzania were then placed in the sand. The pots were then arranged in a randomised split-plot design within four replicate blocks: cutting height (0.15 or 0.30 m) and harvest (first and second harvest) on the main plot and final defoliation level on the sub-plot (0, 25, 50, 75, 100 % leaf area removal) within a controlled environment room (Conviron, Winnipeg, Canada). Seeds were allowed to germinate for three days in the dark at 30 °C with a relative humidity of 90 %. During this period the sand was kept moist with deionised water at all times.

After germination, the plants were grown with a 12-h photoperiod of 500 µmol $m^{-2} s^{-1}$ photosynthetic active radiation (PAR) at plant height and a constant relative humidity of 60 %. The temperature was 30 °C during light hours and 26 °C in the dark. Three weeks after germination, the pots were thinned to three germinated seedlings. Subsequently, the three *P. maximum* plants within each pot constituted a replicate; whilst each pot was the experimental unit, a decision was taken to present results on a per unit plant basis to facilitate comparison with previous studies. Pots were watered to field capacity three times a week with a complete nutrient solution identical to that used by Thornton et al. (1993), except that N was supplied at 1.5 mol m^{-3} NH_4NO_3. Approximately, 18 mol of NH_4NO_3 per pot were supplied to the plants during the experiment.

Initial defoliation to fixed heights

Defoliation was started four weeks after germination. Plants were then cut weekly to a height of either 0.15 m or 0.30 m above the sand surface for seven weeks. Generally, the 0.15 m treatment removed almost all the leaf area and some meristematic tissues on each occasion, whilst with the 0.30 m treatment part of the leaf area was retained and no meristematic tissue was removed.

Final defoliation to remove leaf area percentages

Eight weeks after the first defoliation, all plants were defoliated for a final time to remove 0, 25, 50, 75 or 100 % of the area of each individual leaf blade of the main tiller. From the leaf blade material removed by clipping it was established that for both initial defoliation treatments (0.15 m and 0.30 m) linear relationships existed between the area and fresh weight of the leaf blades. Hence, the proportion by weight of leaf blade removed by clipping was calculated to estimate the proportion removed on an area basis. Actual leaf area removed at final defoliation of *Panicum maximum* plants from each treatment was close to values initially proposed, characterising different levels of final defoliation severity (Table 1). There were therefore ten defoliation treatments in total, with each initial defoliation treatments (fixed cutting height) subjected to one of the five final defoliation treatments (percentage of leaf area removed).

^{15}N labelling, plant harvesting and sample analysis

Immediately following the final defoliation, four replicate pots of each treatment combination were harvested (day 0). Concurrent with this harvest, the nutrient solution was washed from all the remaining non-harvested pots with four changes of 1.0 dm^3 of deionised water to avoid contamination of the new nutrient solution. Pots were then flushed with four changes of a nutrient solution identical to that initially used except all N was enriched with ^{15}N to 5.01 atom % abundance (Cambridge Isotope Laboratories Inc, Andover, USA). Small rings made from coloured-plastic coated wire were used to identify the two youngest visible leaves on the main tiller immediately after the final defoliation (i.e., the two youngest leaves at day 0). The plants were allowed to grow for one further week, during which they received the ^{15}N enriched nutrient solution and after which they were harvested (day 7).

At harvest, roots were separated from the shoot and washed free of sand over a 1mm-mesh sieve with deionised water, resulting in minimal root loss, and then blotted dry with paper towel. The shoot material was separated into side and main tillers. Tillers not previously cut were considered as side tillers. Main tillers were further separated into young leaves, old leaves and stems. Leaf blades with attached sheaths older than the two youngest leaves at day 0 were defined as old leaves, whilst the two youngest leaf blades with attached sheaths at day 0 plus any younger leaves were defined as young leaves. The material remaining at the base of the shoot after all leaves had been removed was defined as stem. All plant material was weighed fresh and after oven drying at 65 °C, and then ball-milled (Retsch, Haan, Germany) prior to analysis. The total N ($^{14}N + ^{15}N$) and ^{15}N concentrations of the samples were determined using a TracerMAT continuous flow mass spectrometer (Finnigan MAT, Hemel Hempstead, UK).

Calculations

N supply was labelled with ^{15}N after final defoliation to distinguish the use of stored N (unlabelled N) from N taken up by root (labelled N) for regrowth. ^{15}N enrichment was used to calculate the uptake of N from the ^{15}N labelled nutrient solution (labelled N) using equations described earlier (Millard and Nielsen, 1989). Net changes on labelled N content of different plant compartments represented allocation of N taken up by root.

Table 1 – Actual percentage of leaf area removed on final defoliation of *P. maximum* plants initially cut to a height of 0.15 or 0.30 m. Values are means (± SE) of four replicates.

Defoliation severity	Leaf area removed %	
(% leaf area)	15 cm	30 cm
0 %	0 ± 0	0 ± 0
25 %	24 ± 1	27 ± 1
50 %	46 ± 2	52 ± 2
75 %	66 ± 5	76 ± 2
100 %	100 ± 0	100 ± 0

The difference between the total and labelled N contents was designated unlabelled N and was assumed to be the N present within the plants at day 0. There was no difference in the unlabelled N content of whole plants between those harvested on day 0 and day 7, N mobilisation was therefore calculated considering the plant as a closed system for unlabelled N over this period. For each treatment, the content of unlabelled N and its partitioning between the various plant compartments on day 0 and day 7 were established from plants harvested on those days. It was assumed that plants of the same treatment, subsequently harvested on day 7, had the same partitioning of unlabelled N on day 0 as the plants actually harvested on day 0. Therefore, for the individual plants harvested on day 7, the unlabelled N contents of the plant components on day 0 and day 7 could be established. Any increase in the unlabelled N content of a plant compartment between day 0 and day 7 represented mobilisation of N to the compartment from other plant parts. Similarly a decrease in unlabelled N represented mobilisation out of the compartment (Thornton et al., 1993; Thornton et al., 1994).

The relative contribution of N from root uptake (uptake) and from mobilisation of stores (mobilisation) for new growth of young leaves and side tillers was calculated by:

$$\text{Uptake (\%)} = (\{LabN_7\text{-}LabN_0\}/\{TotalN_7\text{-}TotalN_0\})*100$$
$$\text{Mobilisation (\%)} = (\{UnlabN_7\text{-}UnlabN_0\}/\{TotalN_7\text{-}TotalN_0\})*100$$

where $LabN_0$ and $LabN_7$ refer to labelled N content of plant compartment on days 0 and 7, respectively; $UnlabN_0$ and $UnlabN_7$ refer to unlabelled N content of plant compartment on days 0 and 7, respectively; $TotalN_0$ and $TotalN_7$ refer to total N content of plant compartment on days 0 and 7, respectively.

Specific uptake of N (SUN) was calculated as the amount of N captured per mean root dry mass by:

$$SUN = (LabN_7\text{-}LabN_0)/((RDM_0 + RDM_7)/2),$$

where $LabN_0$ and $LabN_7$ refer to labelled N content of plants on days 0 and 7, respectively; and RDM_0 and RDM_7 refer to roots dry mass on days 0 and 7, respectively.

Statistical analysis

All statistical analyses were performed using the SAS system (SAS Institute, 2003). Analysis of variance (ANOVA) was conducted to assess whether differences were significant, and the Tukey test was used to compare treatment means. Since the plants harvested on day 0 had not received the ^{15}N enriched nutrient solution, only results from day 7 were used for labelled N analysis. The data were transformed prior to analysis whenever the assumptions of ANOVA were violated. Since the transformation did not affect interpretation of results, untransformed data are presented for clarity.

Results

Plants initially cut to a 0.30 m height had higher whole plant dry mass ($p < 0.05$) than those cut to a 0.15 m height, because of the greater weight of all plant components. Young leaves dry mass increased between day 0 and day 7. Interaction between height and harvest was not significant for whole plant dry mass. All defoliation treatments achieved increases in whole plant and side tillers dry mass throughout harvests on day 0 and day 7 ($p < 0.05$), with the exception of the 100 % defoliation level (Figure 1A, B). Also, no increase of stem dry mass was observed in the 75 and 100 % defoliation level treatments (Figure 1C). The roots' dry mass increased from day 0 to day 7 just in the 50 % defoliation level treatment ($p < 0.05$, Figure 1D). The dry mass of old leaves did not change from day 0 to day 7, but it decreased for old leaves and young leaves ($p < 0.05$) as final defoliation severity increased.

Total N content and unlabelled N of whole plants and their individual compartments were higher for

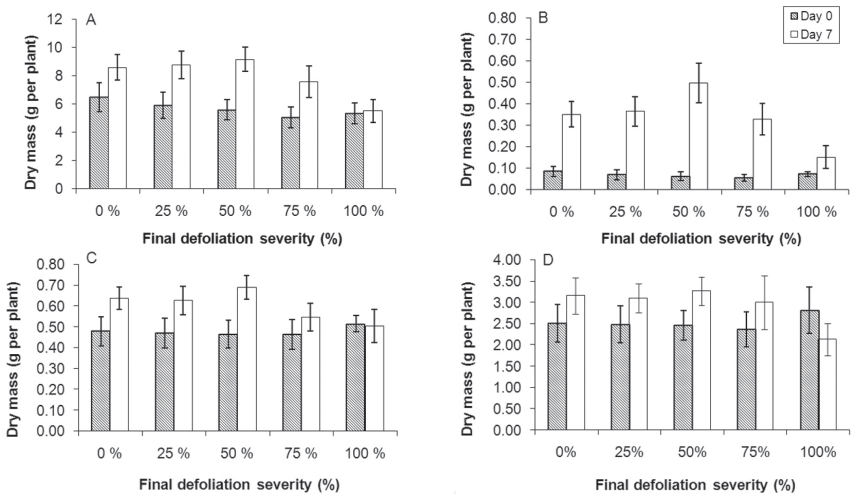

Figure 1 – Effect of final defoliation severity and day of harvest on dry mass of (A) whole plant, (B) side tillers, (C) stems and (D) roots of *P. maximum*. Values represent the means of four replicates and two initial cutting heights. Bars represent standard error of the mean.

the 0.30 m than for the 0.15 m initial cutting height ($p < 0.05$; Table 2). Increase in total N content of whole plants between day 0 and day 7 was lower in the 100 % defoliation treatment than in the other final defoliation treatments.

For both 0.15 and 0.30 m cutting heights, the labelled N of whole plants was lower when the plants were completely defoliated than when less than 100 % of the leaf area was removed. There was no effect of cutting height on the labelled N content of whole plants when either 0 % or 100 % of leaf area was removed during final defoliation. On the other hand, the labelled N of plants subjected to an intermediate defoliation severity (25, 50 or 75 % of leaf area removed during final defoliation) was higher when the plants were previously cut to a 0.30 m height than when they were cut to a 0.15 m height.

Changes in total N content of individual plant compartments also occurred between harvests (Figure 2). Old leaves of *P. maximum* were net sources of N when plants were subjected to more lenient defoliation treatments ($p < 0.05$; 30 cm initial cutting height combined with less than 50 % leaf area removal during final defoliation and 0.15 m initial cutting height combined with less than 25 % leaf area removal during final defoliation). Young leaves and side tillers were net sinks of N ($p < 0.05$), except by plants initially cut to a 0.15 m height and completely defoliated on day 0 where no net change on N content was observed for side tillers (Figure 2). In side tillers and young leaves, the increase of total N was higher for plants receiving a final defoliation of intermediate severity. On the other hand, for stems and roots changes in total N content between harvests were higher in the lower defoliation level treatments ($p < 0.05$; Figure 2).

Changes in the net N content of plant compartments described above represent the overall change in N due to both uptake and its allocation and remobilisation of N. Labelled N in young leaves and side tillers was higher with final defoliation of intermediate severity ($p < 0.05$; Figure 3). In stems and roots, labelled N uptake increased as final defoliation level decreased ($p < 0.05$; Figure 3). There was no difference between the final defoliation severity treatments on the labelled N content of old leaves, but labelled N content of old leaves was higher for initial cutting height of 0.30 m compared with 0.15 m. Labelled N was allocated mainly to young leaves (45.9 to 69 % of labelled N content in whole plants), followed by roots (14 to 31 % of labelled N content in whole plants) (Figure 3). The relative allocation of labelled N to side tillers was higher in plants initially cut to a height of 0.30 m (7.4 to 14.0 % of labelled N content in whole plants) than to 0.15 m (3.6 to 8.9 % of labelled N content in whole plants) (Figure 3).

Specific uptake of N was higher for plants initially cut to a height of 0.15 m than 0.30 m. Specific uptake of N was lower for plants subjected to 100 % leaf area removal treatment than for those from the other final defoliation treatments.

Table 2 – Total N content and unlabelled N of whole plants and individual plant compartments for *P. maximum* initially cut to a height of 0.15 or 0.30 m. Values are means (±SE) of four replicates and two harvest.

	Total N content		Unlabelled N	
	g per plant			
	15 cm	30 cm	15 cm	30 cm
Whole plant	55.2 ± 3.4	81.2 ± 4.4	36.9 ± 1.7	61.1 ± 2.6
Young leaves	24.6 ± 2.3	30.4 ± 2.7	13.3 ± 0.9	19.4 ± 1.3
Side tillers	2.2 ± 0.3	4.9 ± 0.7	0.9 ± 0.1	2.7 ± 0.3
Old leaves	8.6 ± 0.5	15.5 ± 1.0	8.0 ± 0.5	14.2 ± 1.0
Stems	4.9 ± 0.2	6.9 ± 0.2	3.5 ± 0.2	5.5 ± 0.2
Roots	14.8 ± 0.9	23.6 ± 1.2	11.2 ± 0.7	19.2 ± 0.8

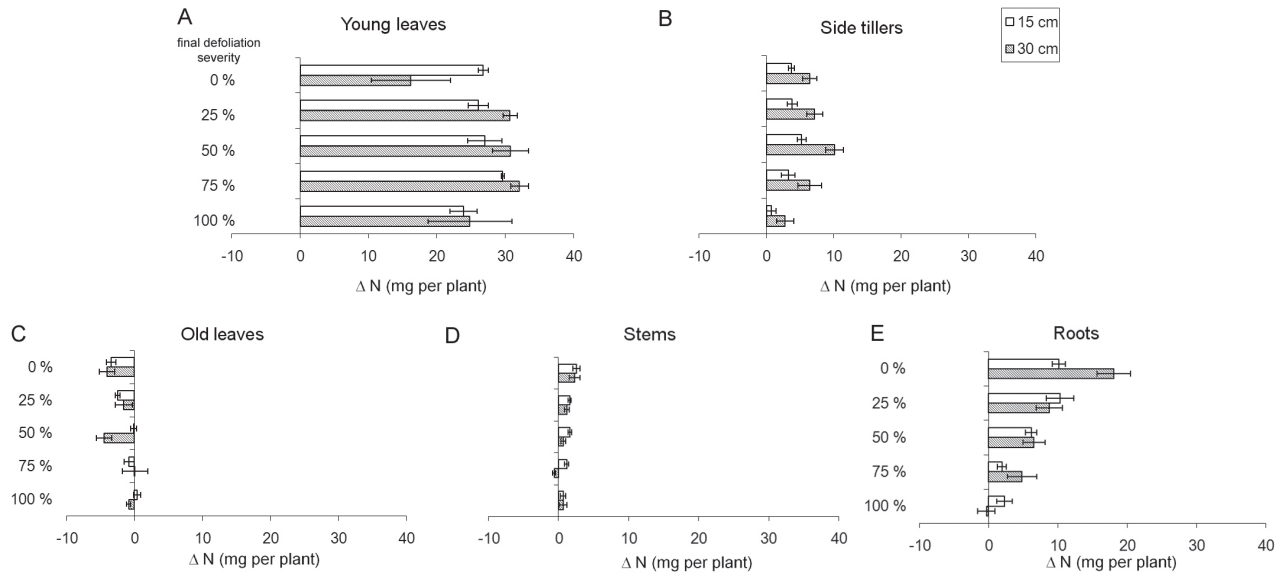

Figure 2 – Changes in total N content of (A) young leaves, (B) side tillers, (C) old leaves, (D) stems and (E) roots of P. maximum over a 7-day period following final defoliation. Values are means (±SE) of four replicates.

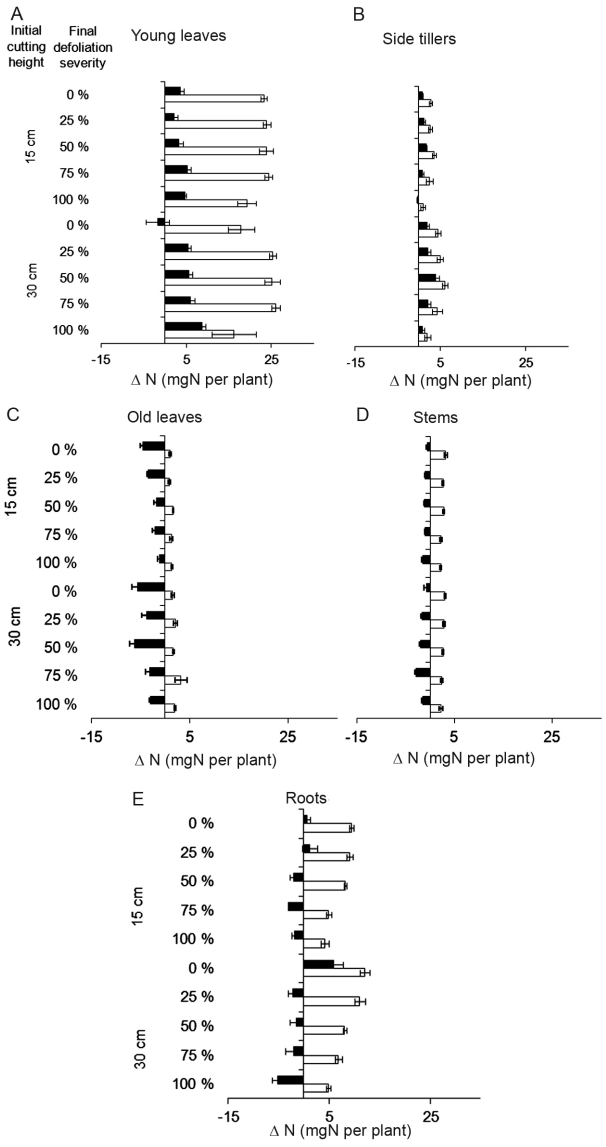

Figure 3 – Changes in labelled (□) and unlabelled (■) N of (A) young leaves, (B) side tillers, (C) old leaves, (D) stems and (E) roots of *P. maximum* over a 7-day period following final defoliation. Values are means (±SE) of four replicates.

In most instances, young leaves were the main sink for mobilised N, followed by side tillers (Figure 3). The exceptions to this were young leaves of plants originally cut to 0.30 m receiving a final defoliation of 0 % and side tillers of plants originally cut to 0.15 m receiving 100 % final defoliation (Figure 3). In these instances, the unlabelled N contents decreased, suggesting mobilisation out of these compartments. In all treatments old leaves and stems were sources of mobilised N ($p < 0.05$). The relative contribution of old leaves to N mobilisation was higher in plants initially cut to a height of 0.30 m than to 0.15 m and decreased as defoliation intensity increased (Figure 3). On the other hand, roots became a source of N for mobilisation just when plants were defoliated on day 0 (Figure 3).

In all treatments for both young leaves and side tillers, current root uptake (labelled N) supplied more N than mobilisation (unlabelled N) (Table 3). Generally, the relative contribution of root uptake to the total N increase was greater in young leaves than side tillers and the importance of N remobilisation for new growth was greater at the 0.30 m cutting height (except in young leaves of plants originally cut to 0.30 m receiving a final defoliation of 0 %) (Table 3).

Discussion

Nitrogen uptake

Changes in total N content of whole plants occurred due to labelled N uptake. Labelled N of whole plants was lower when the plants were completely defoliated (100 % final defoliation treatment), probably due to a negative effect of defoliation on root dry mass and specific uptake of N. Additionally, since all leaf area was removed, low soil N flux induced by lower plant transpiration may also have contributed to a reduction of N uptake of plants from the 100 % defoliation treatment (Durand et al., 2010).

Lestienne et al. (2006) observed a reduction in N uptake of *Lolium perenne* with the removal of more than 75 % leaf area when N supply was high and suggested this was related to a negative effect of defoliation intensity on root dry mass. In the present experiment, negative effects of complete defoliation on root dry mass of *P. maximum* plants receiving a high supply of N were also observed. The root dry mass of plants where 100 %

Table 3 – Relative use of either uptake or remobilisation to supply N for new growth of young leaves and side tillers of *P. maximum* over a 7-day period following final defoliation. Values are means (±SE) of four replicates.

Cutting height	Defoliation severity	Young leaves		Side tillers	
		Uptake	Mobilisation	Uptake	Mobilisation
cm	%				
15	0	87 ± 3	13 ± 3	76 ± 10	24 ± 10
15	25	92 ± 3	8 ± 3	71 ± 6	29 ± 6
15	50	88 ± 3	12 ± 3	68 ± 4	32 ± 4
15	75	82 ± 2	18 ± 2	76 ± 9	24 ± 9
15 [1]	100	80 ± 2	20 ± 2	-	-
30 [1]	0	-	-	69 ± 6	31 ± 6
30	25	82 ± 2	18 ± 2	69 ± 6	31 ± 6
30	50	82 ± 2	18 ± 2	61 ± 5	39 ± 5
30	75	81 ± 2	19 ± 2	67 ± 9	33 ± 9
30	100	65 ± 8	35 ± 8	72 ± 15	28 ± 15

[1]On young leaves of plants originally cut to 0.30 m receiving a final defoliation of 0 % and side tillers of plants originally cut to 0.15 m receiving a final defoliation of 100 %, there was a net decrease of unlabelled N.

leaf area was removed did not increase between day 0 and day 7, suggesting a decrease on root growth and/or an increase on root senescence during this period. On the other hand, Lestienne et al. (2006) observed an increased specific uptake of N when defoliation severity increased from 0 to 100 % leaf area removal and suggested that changes in root morphology could partially explain these results. These results differ from those observed in the present experiment, where complete defoliation of *P. maximum* plants reduced specific uptake of N. A negative effect of defoliation on root growth and/or senescence rate may in part explain the reduced specific uptake of N observed on completely defoliated plants, as young roots seems to have an important role on nutrients uptake (Taiz and Zeiger, 2010).

An increase on specific N uptake was observed on plants initially cut to a 0.15 m height. In spite of that, labelled N content in plants initially cut to a 0.30 m was higher than in those initially cut to a 0.15 m height when subjected to an intermediate defoliation severity (25 to 75 % leaf area removal during final defoliation), probably due to the higher root dry mass of plants from the 0.30 m treatment. Increased specific N uptake was not enough to compensate for reduction on root dry mass in plants initially cut to a 0.15 m height when 25, 50 or 75 % of leaf area was removed on final defoliation. These results are in agreement with those observed by Thornton and Millard (1996) for *L. perenne* and *P. trivialis* where the increased N uptake per unit of root dry weight due to an increased severity of repeated defoliation did not offset the reduction of root mass.

The initial cutting height of 0.15 m and 0.30 m only had a subsequent effect on N uptake of *P. maximum* when the plants were subject to further defoliation, i.e. the effect of previous defoliation history on N uptake is dependent upon the severity of a single additional defoliation. Any management strategy of *P. maximum* swards aimed at maximising fertiliser use efficiency would need to take account of such effects.

P. maximum does not sustain heavy defoliation on areas characterised by low soil fertility. The increase of N supply in *P. maximum* improves dry mass production of thin roots and increases total root surface area (Silveira and Monteiro, 2011). In the present experiment, plants subjected to 100 % leaf area removal on final defoliation had a lower increase on whole plant total N content, a reduced N uptake and a lower specific N uptake. Heavy defoliation thus reduces root activity in *P. maximum*, a plant species which we have shown depends mainly on N from root uptake to guarantee regrowth. This effect may be exacerbated in low input systems growing *P. maximum* where root uptake of N may already be limited.

Nitrogen allocation

The total N content of young leaves and side tillers increased during the week following final defoliation. These results support those obtained by Santos et al. (2002), who observed that the same plant components were the main sinks for N in undefoliated *Panicum maximum* plants. Overall, the increases in total N content of young leaves and side tillers were greater for plants originally cut to 0.30 m compared with those cut to 0.15 m and for plants receiving a final cut of intermediate severity compared to plants where the final defoliation removed either 0 % or 100 % of the leaf area. The smaller increase in total N of young leaves and side tillers in plants where 0 % of the leaf area was removed suggests that defoliation stimulates new growth of this plant component.

The labelled N in young leaves and side tillers was higher with a final defoliation of intermediate severity, whilst in stems and roots labelled N increased as final defoliation level decreased. Lestienne et al. (2006) observed no effect of final defoliation intensity on labelled N allocated to growing leaves of *Lolium perenne*, but also found a decrease in labelled N allocated to roots when 100 % leaf area was removed.

The main sink for labelled N in the actual experiment was young leaves, followed by roots and side tillers. Santos et al. (2002) also observed that young leaves, side tillers and roots were sinks for N from root uptake of undefoliated *P. maximum* plants, indicating that defoliation does not change the relative sink strength of the various components of *P. maximum* for N derived from root uptake. On the other hand, source/sink relations for stored N in *P. maximum* seems to depend on defoliation. Santos et al. (2002) observed that mobilised N increased just in young leaves and side tillers of undefoliated *P. maximum* plants whilst no changes on unlabelled N of roots compartments were observed. In the present experiment, roots were source of N for mobilisation just when plants were defoliated on day 0 and became a sink for mobilized N when plants initially cut to a 0.30 m height were not subjected to a final defoliation (0 % leaf area removal on day 0).

Lestienne et al. (2006) observed that roots were a net source of N and that increasing defoliation severity of *L. perenne* did not change the amount of N mobilised to young leaves, reliant on an increase in the contribution of roots supplying mobilised N to growing leaves. Taken together results of Lestienne et al. (2006) and the current study suggest a different effect of defoliation on source/sink relations of *P. maximum* and *L. perenne*. In *L. perenne* roots are always a source of N while in *P. maximum* its behaviour as source or sink for mobilized N depends on defoliation treatment. Whether these differences represent general differing strategies between C3 and C4 plants would require further species to be investigated.

P. maximum seems to behave following the grazing optimization hypothesis. The grazing optimization hypothesis predicts that grazing at intermediate intensities stimulates plant production and enhances net primary production of grazed plants above ungrazed plants (McNaughton, 1979). Positive effects of herbivory on plant performance are related to: (i) modification of light availability; (ii) reduction of water loss

and water stress; (iii) accelerated or regulated nutrient cycling; (iv) biomass allocation; and (v) improvement of the photosynthetic rate in tissues remaining or produced after grazing (Leriche et al., 2001). Results presented here for *P. maximum* suggest that plasticity of N uptake and allocation due to defoliation may be related to increased net primary herbage production of grazed when compared to ungrazed plants and that the effect of defoliation over plants N dynamics and its relationship with the grazing optimization hypothesis is worthy of further study.

Source of N for new growth: N mobilisation × N uptake

All the treatments for both young leaves and side tillers current root uptake supplied more N than mobilisation. These results are in agreement with Santos et al. (2002), who observed that root uptake was the major source of N for growing leaves of intact *P. maximum*. Generally, the relative contribution of root uptake to the total N increase was greater in young leaves than side tillers, indicating that the allocation pattern of mobilised N differed from that of N derived from current root uptake. These confirms previous results from Santos et al. (2002), who observed differences in allocation pattern of mobilised N and N from root uptake in undefoliated *P. maximum* plants.

Conclusions

Adaptation of *P. maximum* to defoliation is related to plasticity of N uptake, mobilisation and allocation, but changes in N dynamics does not offset negative impacts of complete defoliation of *P. maximum* plants.

Acknowledgements

The financial support of FAPESP and the Scottish Government through the Rural and Environment Research and Analysis Directorate (RERAD) is gratefully acknowledged.

References

Aldana, B.R.V.; Berendse, F. 1997. Nitrogen-use-efficiency in six perennial grasses from contrasting habitats. Functional Ecology 11: 619–626.

Andrade, C.M.S.; Garcia, R; Couto, L.; Pereira, O.G. 2001. Factors limiting the growth of *Panicum maximum* cv. Tanzania-1 in an agrosilviopastoral system with eucalypt, in the Cerrado of Minas Gerais, Brazil. Revista Brasileira de Zootecnia 30: 1178–1185 (in Portuguese, with abstract in English).

Durand, J.L.; Gonzalez-Dugo, V.; Gastal, F. 2010. How much do water deficits alter N nutrition status of forage crops? Nutrient Cycling Agroecosystem 88: 231–243.

Gastal, F.; Dawson, L.A.; Thornton, B. 2010. Responses of plants traits of four grasses from contrasting habitats to defoliation and N supply. Nutrient Cycling Agroecossystems 88: 245–258.

Leriche, H.; LeRoux, X.; Gignox, J.; Tuzet, A.; Fritz, H.; Abbadie, L.; Loreau, M. 2001 Which functional process control the short-term effect of grazing on net primary production in grasslands? Oecologia 129: 114–124.

Lestienne, F.; Thornton, B.; Gastal, F. 2006. Impact of defoliation intensity and frequency on N uptake and mobilisation in *Lollium perenne*. Journal of Experimental Botany 57: 997–1006.

Matthew, C.; Assuero, S.G.; Black, C.K.; Sackville Hamilton, N.R. 2000. Tiller dynamics of grazed swards. p. 127–150. In: Lemaire, G.; Hodgson, J.; Moraes, A.; Carvalho, P.C.F.; Nabinger, C., eds. Grassland ecophysiology and grazing ecology. CABI, Wallingford, UK.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. The American Naturalist 113: 691–703.

Millard, P.; Nielsen, G.H. 1989. The influence of N supply on the uptake and remobilisation of stored N for the seasonal growth of apple trees. Annals of Botany 63: 301–309.

Muir, J.P.; Jank, L. 2004. Guineagrass. p. 589–621. In: Moser, L.E.; Burson, B.L.; Sollenberger, L.E., eds. Warm-season (C_4) grasses. American Society of Agronomy/ Crop Science Society of America/Soil Science Society of America, Madison, WI, USA.

SAS 2003. Institute. System for Microsoft Windows, Release 9.1. SAS Institute, Cary, NC, USA. (CD ROM).

Santos, P.M.; Thornton, B.; Corsi, M. 2002. N dynamics in the intact grasses *Poa trivialis* and *Panicum maximum* receiving contrasting supplies of N. Journal of Experimental Botany 53: 1–10.

Schnyder, H.; Schäufele, R.; Visser, R.; Nelson, C.J. 2000. An integrated view of C and N uses in the leaf growth zones of defoliated grasses. p. 41–60. In: Lemaire, G.; Hodgson, J.; Moraes, A.F.; Carvalho, P.C.; Nabinger, C., eds. Grassland ecophysiology and grazing ecology. CABI, Wallingford, UK.

Silveira, C.P.; Monteiro, F.A. 2011. Influence of nitrogen and calcium fertilizations on morphological and productive characteristics of tanzania guineagrass roots grown in nutrient solution. Revista Brasileira de Zootecnia 40: 47–52 (in Portuguese, with abstract in English).

Taiz, L.; Zeiger, E. 2010. Plant Physiology. 5ed. Sinauer, Sunderland, MA, USA.

Thornton, B.; Millard, P.; Bausenwein, U. 2000. Reserve formation and recycling of carbon and N during regrowth of defoliated plants. p. 85–99. In: Lemaire, G.; Hodgson, J.; Moraes, A.F.; Carvalho, P.C.; Nabinger, C., eds. Grassland ecophysiology and grazing ecology. CABI, Wallingford, UK.

Thornton, B.; Millard, P.; Duff, E.I. 1994. Effects of nitrogen supply on the source of nitrogen used for regrowth of laminae after defoliation of four grass species. New Phytologist 128: 615–620.

Thornton, B.; Millard, P.; Duff, E.I.; Buckland, S.T. 1993. The relative contribution of remobilisation and root uptake in supplying N after defoliation for regrowth of laminae in four grass species. New Phytologist 124: 689–694.

Thornton, B.; Millard, P. 1996. Effects of severity of defoliation on root functioning in grasses. Journal of Range Management 49: 443–447.

Volenec, J.J.; Ourry, A.; Joern, B.C. 1996. A role for N reserves in forage regrowth and stress tolerance. Physiologia Plantarum 97: 185–193.