Effects of Temperature, Nitrogen Fertilisation and Leaf and Tiller Age on Specific Leaf Area of *Brachiaria decumbens*

J. Busqué
University of Edinburgh, UK

M. Herrero
International Livestock Research Institute, Kenya

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EFFECTS OF TEMPERATURE, NITROGEN FERTILISATION AND LEAF AND TILLER AGE ON SPECIFIC LEAF AREA OF *BRACHIARIA DECUMBENS*

J. Busqué[1] and M. Herrero[1,2]

[1]Institute of Ecology and Resource Management, University of Edinburgh, West Mains Rd. EH9 3JG, Edinburgh, UK.

[2]International Livestock Research Institute (ILRI), P. O. Box 30709, Nairobi, Kenya

Abstract

Signal grass (*Brachiaria decumbens* Stapf) micro-swards were grown under controlled environmental conditions at different temperatures and nitrogen fertilisation rates. Specific leaf area was responsive both to temperature and nitrogen, but did not change with the level of insertion of the leaf in the tiller. Senescing leaves had higher specific leaf area than old extended green leaves and these had higher values than new extended green leaves. Changes in specific leaf area were more related to changes in leaf area and more exactly to changes in leaf width.

Keywords: Signal grass, leaf weight, leaf length, leaf width, leaf number.

Introduction

Specific Leaf Area (SLA: leaf area per unit of leaf dry matter weight) is one of the main variables affecting plant growth, mainly through changes in leaf area ratio (i.e. ratio of leaf area to total plant dry weight) and photosynthetic nitrogen-use efficiency (Bultynck *et al.* 1999). Studying the factors affecting SLA is of primary importance for understanding and predicting the growth responses of tropical grasses to different environmental and management regimes The main objective of this experiment was to study the responses of SLA to temperature, nitrogen and leaf and tiller age.

Material and Methods

Signal grass (*Brachiaria decumbens* Stapf) micro-swards were grown on wooden trays of 0.24 m^2 of area and 0.10 m of depth, under controlled environments (760 μmol m^{-2} s^{-1} of PAR, constant 12/12h day/night length and relative humidity of 75%). Each micro-sward was assigned to a fixed nitrogen fertilisation regime throughout the whole experiment, equivalent to 0, 100 or 200 kg N ha^{-1} yr^{-1} (0N, 100N, 200N). After a preliminary growth period of 50 days at 30^{o}C day / 25^{o}C night, micro-swards were cut at a height of 5 cm (fixed cutting height throughout the whole experiment) and allocated to one of three day temperatures: 25, 30 and 35^{o}C. Night temperatures were common in all cases: 25^{o}C. All micro-swards were watered daily to field capacity. Two regrowth periods of 50 and 48 days of duration were studied, each period ending with the cutting of the micro-swards and their allocation to a new room or temperature regime. Measurements of leaf fresh and dry weight, length and blade area were made destructively at the end of each regrowth period from marked tillers. Each leaf was classified according to its development as newly appeared R, expanding X, expanded and green $E_{1,2}$, senescing S or dead D. Expanded green leaves were further distinguished within the tiller as youngest (1) or any of the rest (2). Leaves were also identified by their number in ascending order from the first appeared leaf in the tiller (leaf number 1).

A general linear model was used for analysing the data. The model was:

$$Y_{ijklm} = P_i + N_j + T_K + U_l + D_m + e$$

where *Y* corresponded to the response variable: SLA, leaf dry weight, leaf area, leaf length and estimated width. *P* was one of the two regrowth periods. *N* was the nitrogen dose. *T* was the temperature regime, *U* was the leaf number, *D* was the leaf developmental stage and *e* was the unexplained variance. Interactions between the main effects were considered when they were statistically significant ($P<0.05$). Estimated width was calculated dividing leaf area by leaf length.

Results and Discussion

SLA mean values were lower than previously reported for signal grass (Giraldo *et al.* 1998) and other tropical grasses (Ivory and Whiteman, 1978). These discrepancies were probably caused by the comparatively lower N fertilisation rates of the present study, since it has been observed that SLA increases with N fertilisation in fast growing grasses (Van der Werf *et al*. 1993). Nevertheless, the values obtained in the present study may reflect more accurately the SLA of signal grass grown under natural savanna or cerrado conditions throughout Latin America, where soils can be severely nutrient depleted.

Linear and area leaf measures were mainly determined by the developmental stage of the leaf (due to the smaller and contrasting values observed for R and X leaves), and to a lesser extent by leaf number and the treatments (Table 1). Leaf dry weight changed similarly with leaf number and developmental stage but was not affected by the treatments. Temperature had an effect on SLA, while SLA did not change with the level of the insertion of the leaf.

SLA changes with treatment and intrinsic tiller development were analysed considering its components leaf area and dry weight relative to the minimum values of each effect (except in the case of leaf development, where the reference was the E_1 leaves). Changes in leaf area were further analysed to study the relative importance of leaf width and length changes (Table 2).

At 200N SLA increased due to increases in leaf area and the stability in leaf weight. The increase in leaf area was caused by an increase in leaf length. SLA increases with nitrogen have been seen to occur in fast growing grasses, like signal grass, in comparison with slow growing grasses (Van der Werf *et al.* 1993).

The maximum SLA value was obtained at 30^{o}C due to the high increase in leaf area. As with nitrogen, the increase in leaf area was caused by an increase in leaf length. The decrease in SLA at 35^{o}C was related to the decrease in leaf area, mainly through a decrease in leaf width. Leaf weight remained constant at all temperatures. In Kikuyu grass (*Pennisetum clandestinum*) SLA increased from 15 to 20^{o}C and remained with similar values until 30^{o}C. In this case both leaf area and leaf weight increased from 15 to 25^{o}C (Murtagh *et al.* 1987).

No change was observed in SLA with level of leaf insertion in the tiller, though it tended to decrease from leaf 5 onwards. Leaf weight increased linearly with leaf number and leaf area increased until leaf 7 and decreased for leaf 8. Leaf length increased linearly until leaf 7, but the proportional increase was small, and fell significantly for leaf 8. Leaf width increased more than leaf length though its trend with leaf number was not linear but similar to that of leaf area. Wilson (1976) observed similar SLA values for most of the leaves in high rank tillers of *Panicum maximum* var. *trichoglume*. Tendencies in leaf weight, area, length and width were also similar to those of this experiment.

Senescing leaves (S) had the highest SLA values, corresponding to the highest leaf area and high leaf weight values. The increase in leaf width was relatively more important than that of leaf length in its contribution to the increase in leaf area. Old green extended leaves (E_2) showed a tendency to have higher SLA than E_1, as leaf area increased (slightly higher increase in leaf width than leaf length) slightly more than leaf weight.

We conclude that SLA values were generally low, presumably because of the low fertilisation levels of the experiment. For the size range and type of tillers studied, SLA remained constant with leaf number. Therefore, increases in plant growth efficiency with tiller size must be mediated by other factors. For example, in the same experiment we observed that the number of live leaves per tiller increased until the appearance of leaf 7. Temperature and nitrogen level changed SLA mainly through changes in leaf area and in most cases due to changes in leaf width: for extended green leaves (E_1 and E_2) SLA showed the highest correlation ($r^2 = 0.78$) with the estimated width, much higher than with any of the other response variables.

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Table 1 - Statistical significance (***=P<0.01; **=P<0.05) and percentage of the model explained (%m) by the effects of nitrogen, temperature and by leaf number and leaf developmental phase (using adjusted sum of squares) on leaf length, estimated leaf width, leaf area, leaf dry weight and specific leaf area of *Brachiaria decumbens*.

	Length		Width		Area		DW		SLA	
	P	%m	P	%m	P	%m	P	%m	P	%m
Nitrogen	**	2.0	***	6.9	***	5.2	NS	0.7	***	7.9
Temperat.	***	5.5	***	5.8	***	7.7	NS	0.3	***	22.4
Leaf no.	***	6.1	***	10.8	***	11.4	***	44.4	NS	1.6
Leaf devel.	***	52.4	***	61.5	***	50.4	***	35.4	***	47.1
R^2 model	57%		67%		68%		63%		73%	
n	416		227		380		283		232	

Table 2 - Least square means of leaf length, estimated leaf width, leaf area, leaf dry weight and specific leaf area by each of the fixed effects analysed. Different letters among levels of the same effect represent statistically significant different means (Tukey's test with a 95% confidence interval).

	Level	Leaf length (mm)	Est. Leaf width (mm)	Leaf Area (cm^2)	Leaf DW (mg)	SLA (cm^2 gr^{-1})
Nitrogen	0N	102.9 a	3.15 a	3.90 a	35.7 a	98.08 a
	100N	103.5 ab	2.18 b	3.16 a	32.7 a	73.83 b
	200N	112.7 b	3.33 a	5.05 b	36.8 a	125.24 c
Temperat.	25^{o}C	99.1 a	3.02 a	3.46 a	33.6 a	101.35 a
	30^{o}C	117.3 b	3.33 a	5.54 b	35.6 a	125.10 b
	35^{o}C	102.6 a	2.30 b	3.12 a	36.0 a	70.70 c
Leaf number	3	93.1 a	1.75 a	2.51 a	15.8 a	103.06 a
	4	104.1 a	2.36 ab	3.48 b	25.2 b	105.50 a
	5	108.1 b	2.86 bc	4.25 c	32.7 c	105.30 a
	6	112.9 b	3.35 c	4.79 c	40.1 d	102.54 a
	7	116.3 b	3.56 c	5.05 c	44.0 de	95.07 a
	8	103.7 a	3.44 c	4.14abc	52.7 e	82.84 a
Leaf development	R	69.0 a	0.48 a	0.40 a	14.6 a	37.24 a
	X	99.9 b	1.93 b	2.63 b	30.9 b	71.24 be
	E_1	103.2 b	3.31 c	4.18 c	35.8 b	109.26 c
	E_2	114.5 bc	3.93 cd	5.21 d	42.6 bc	115.72 bcd
	S	120.1 c	4.24 d	5.81 d	41.9 c	134.34 d
	D	131.5 c	3.41bcd	5.98 cd	44.6 c	126.51ce