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Effects of End of Dry Season Shoot Removal on the Growth of Three Savanna Grasses with Different Phenologies[1]

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ABSTRACT

This paper presents the results of a field experiment investigating the effects of shoot removal at the end of the dry season on tillering and aerial biomass in three perennial savanna grasses. The experiment was intended to simulate the effects of savanna fires at the end of the dry season. The experiment included three initial size classes of plants that were allowed to grow free from competitors. The results showed an immediate negative effect of shoot removal on tiller number in all three species; however, at the end of the experiment, defoliated plants had recovered and their final sizes did not differ significantly from those of control plants. We registered an overcompensating response to shoot removal on aerial biomass of *Trachypogon plumosus*, while the other two species (*Andropogon semiberbis* and *Leptocoryphium lanatum*) compensated completely for the removed aerial biomass. Differences in initial plant size were only significant in *L. lanatum*. Shoot removal resulted in a significant decrease in the fraction of flowering tillers in *T. plumosus*, but had no significant effects on flowering in *A. semiberbis*. Experimental plants of *L. lanatum* did not flower during the experiment. Although inmediate shoot removal effects were strongly negative, the three species were able to recover not only in the number of tillers but also in aerial biomass. Based on the differences between actual burning and experimental removal of shoots, we expect that the compensating responses to actual fire would be greater than the ones resulting from this study.

RESUMEN

Se presentan los resultados de un estudio experimental sobre los efectos de la remoción total de la biomasa aérea sobre la dinámica de los vástagos y el crecimiento de la biomasa aérea en tres especies de gramíneas de la sabana. La remoción, efectuada a ras del suelo a finales de la estación seca, simula los efectos de remoción de la biomasa aérea por el fuego. Se incluyeron tres clases de tamaños iniciales y las plantas crecieron libres de competencia. Los resultados muestran una inmediata respuesta negativa de las tres especies al corte, pero al final del experimento seis meses más tarde, las plantas se habían recuperado y su tamaño final no difirió significativamente del controL. En crecimiento de la biomasa aérea, *Trachypogon plumosus* experimentó una sobrecompensación en respuesta al corte, mientras las otras dos especies (*Andropogon semiberbis* y *Leptocoryphium lanatum*) compensaron por la biomasa aérea removida en el corte experimental. El tamaño inicial sólo tuvo efectos significativos en *L. lanatum*. El corte produjo una disminución significativa en la fracción de vástagos florales en *T. plumosus*, pero no tuvo efectos sobre la floración en *A. semiberbis*. *Leptocoryphium lanatum* no floreció en el experimento. Aunque la remoción de vástagos tuvo efectos inmediatos muy negativos, las tres especies se recuperaron, no solo en número de vástagos por planta sinó también en su biomasa aérea. Basados en las diferencias entre la quema y la remoción experimental de los vástagos, esperamos que las respuestas compensatorias al fuego serán mayores que las obtenidas en este estudio.

Key words: clipping; compensatory growth; defoliation; fire; grasses; phenology; savanna; tillering; Venezuela.

THE GROWTH OF PERENNIAL GRASSES in seasonal environments can be evaluated by two distinct attributes: the increase in basal area by tillering throughout the life span of the plant, and the seasonal fluctuations in the above- and belowground biomass as a result of seasonality in the environment. The phenologies of Neotropical savanna grasses have been documented based on seasonal variation in the aboveground biomass (Sarmiento & Monasterio 1983, Raventós & Silva 1988). The phenophase of vigorous tiller growth seems to depend on moisture availability in the topsoil, which in turn depends on seasonal rainfall and the capacity of the soil to store water. Therefore, as the season with available water ends, savanna grasses enter a quiescent phase (Sarmiento 1984). After several weeks of drought, shoots senesce and eventually burn at the end of the dry season.

Grasses from Neotropical savannas differ from

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one another in the patterns of shoot biomass production. Sarmiento (1984) distinguished several phenological groups based on flowering time. Some species (called "precocious" and "early" species) either bloom and then start vegetative growth, or grow rapidly to a plateau and then flower. Other species grow more slowly, reach a plateau, and bloom in mid-season ("intermediate" species); still other species grow even more slowly and reach the plateau and flower at the end of the wet season ("late" species). These phenological differences in the pattern of tiller growth and the time of flowering are related to other plant traits such as aboveground architecture and competitive ability (Silva 1987, Raventós & Silva 1988), shoot/root ratio (Medina & Silva 1990), annual seed crop, and seed dormancy (Silva & Ataroff 1985).

The seasonal pattern of tiller growth is also important relative to plant responses to variability in rainfall and soil moisture availability (Sarmiento 1983a, b) and to other time-variable factors such as fire and grazing (Silva 1987). Tillering of Neotropical savanna grasses has not been subjected to detailed study. Silva & Ataroff (1985), however, have suggested that the patterns of tiller recruitment may differ substantially from those of seasonal tiller growth, especially in "late" species.

Tiller growth and flowering are strongly affected by the occurrence of fire, which usually takes place at the end of the dry season. Fire has two antagonistic effects on the grass populations: it is a direct mortality factor, killing tillers, meristems, and small plants (Canales & Silva 1987; Silva & Castro 1989; Silva *et al.* 1990, 1991); on the other hand, it enhances subsequent grass growth. Growth is stimulated by biomass removal that increases radiation reaching the ground and the release of nutrients by the combustion of the dry biomass (Sarmiento 1984). Since savanna fires act as a defoliating agent, one possible response to burning could be a compensatory effect similar to that reported in response to herbivory (McNaughton 1983). References to compensatory responses are mostly from clipping experiments simulating grazing. In some cases, increased plant growth in response to herbivory can increase plant fitness (Paige & Whitham 1987, Maschinski & Whitham 1989). It is less clear, however, how specific growth conditions influence the ability of the plant to compensate for lost tissues. Belsky (1987) and Maschinski and Whitham (1989) suggest that plants are more likely to overcompensate when water and nutrients are abundant, whereas Oesterheld & McNaughton (1991) predict that overcompensation should tend to occur when plants are under stress. Furthermore, different explanations have been proposed for overcompensation. McNaughton (1986) and Crawley (1987) have proposed that overcompensation evolved as an adaptive response to herbivory. In contrast, Aarssen and Irwin (1991) have proposed that overcompensation is an indirect consequence of selection induced by competition.

The phenological phase of the plant at the moment of defoliation is a key factor in determining plant responses, and the responses also depend on the number, nature, and location of removed meristems (Olson & Richards 1988, Becker *et al.* 1997). Species tolerant of grazing produce greater numbers of fast-growing tillers than do species intolerant of grazing (Caldwell *et al.* 1981, Busso & Richards 1995). We expect savanna grass species with different phenologies and canopy architectures to differ in their responses to shoot removal. These responses may be restricted to tiller growth or to tiller recruitment, or they may include both processes. Furthermore, plant size may play a role in these responses, as has been shown in previous studies (Silva & Castro 1989, Silva *et al.* 1990).

We present results from a study with the goals to: (1) determine the effects of shoot removal at the end of the dry season on tiller recruitment and tiller growth; (2) investigate the role of plant size in these responses; and (3) detect differences among species responses. Shoot removal was intended to simulate the defoliating effects of an end-of-dry-season fire, since burning was not experimentally feasible.

MATERIALS AND METHODS

STUDY SITE.—The study was conducted in an experimental area protected from grazing at the UNELLEZ Botanical Garden in the city of Barinas, Venezuela (38°N, 70°12′W). The area was occupied by typical wooded savanna until *ca* 30 years ago. Mean annual temperature is 27°C, and mean annual rainfall is 1700 mm, with a rainy season from May to November and a dry season from January to April. Burning usually takes place in April, before the rains start.

THE SPECIES.—The species used in the experiment were *Andropogon semiberbis* (Nees) Kunth, *Trachypogon plumosus* (Humb. & Bonpl.) Nees, and *Leptocoryphium lanatum* (H.B.K.) Nees. The species were selected as representative of the three major phenological groups: early, intermediate, and late flowering grasses, that are found in the seasonal savannas of western Venezuela. The species also differ in their architectural patterns: basal versus erect habits, which are briefly described below.

Andropogon semiberbis flowers late in the wet season (November) and has an erect architecture with short rhizomes rising above ground. *Trachypogon plumosus* flowers in the middle of the wet season (September) and has an erect architecture. It produces large tussocks with loose, short rhizomes, and many long rhizomes for clonal growth. *Leptocoryphium lanatum* is a culmless, precocious species flowering in April. Its rhizomes are located deep below ground. Several previous reports on growth, competition, demography, and responses to fire are available for these species (Silva & Ataroff 1985; Silva & Castro 1989; Silva *et al.* 1990, 1991; Raventos & Silva 1995).

FIELD METHODS.—In June of 1989, adult plants were randomly removed from an intact savanna nearby to obtain transplants of different size for each species. After several trials to determine optimal levels of clipping, transplants were successful with *A. semiberbis* (A) plants clipped at 5-cm height, *T. plumosus* (T) plants clipped at 25-cm height, and *L. lanatum* (L) plants clipped at ground level.

Vegetation was removed from an experimental plot (50 × 30 m) by mechanical means, and the plot was squared into subplots (1 × 1 m). We chose three different initial size classes for each species as follows. For *A. semiberbis* and *T. plumosus*: class I: 1 tiller; class II: 5 tillers; class III: 20 tillers. For *L. lanatum*: class I: 1 tiller; class II: 2 tillers; class III: 7 tillers. In this last species, transplant size was smaller than in the other two because not enough plants were available. Single plants were planted randomly at the center of the square. Plantings in each size class were replicated ten times for each species. From July to October of 1989, the plants were monitored weekly, and dead ones were replaced. Plots were weeded monthly by mechanical means throughout the year. In October of 1989, all the plants were successfully established and had reached a similar height within each species. Thereafter, and until October of 1990, plants were monitored monthly and the number of tillers counted. At the end of April 1990, we randomly selected five replicates from each initial size class and clipped them at ground level, simulating the clipping effects of savanna fires. This aerial biomass was dried to constant weight, weighed, and labeled "removed biomass". The other five replicates were used as controls. The aerial biomass of each plant was harvested at the end of October 1990 and labeled "final biomass." The sum of the "removed biomass" and the "final biomass" for each individual plant was called "total biomass."

After flowering of each species, we counted the number of flowering tillers and the total number of tillers for each plant to determine the fraction of tillers flowering.

STATISTICAL ANALYSIS.—We analyzed the effects of shoot removal and initial size on three parameters of vegetative growth (final number of tillers, final biomass, and total biomass per plant) and on reproductive growth (fraction of tillers flowering). For the effects of shoot removal and initial plant size on vegetative growth, we considered each species separately due to the initial differences in the number of tillers between *L. lanatum* and the other two species. The vegetative data were transformed logarithmically before applying a two-way ANOVA (initial size × treatment), followed by a Tukey test to assess significant differences due to plant size and due to treatment (Day & Quinn 1989, Sokal & Rohlf 1995).

To analyze the effects of species, initial size, and shoot removal on the proportion of reproductive tillers per plant, we applied a three-way ANOVA with an aposteriori Tukey test (Day and Quinn 1989). This time we used an arcsine transformation of the data, because this transformation is especially appropriate to percentages and proportions (Sokal & Rohlf 1995). After the logarithmic and the arcsine transformations the data met the assumption of normality fairly well, with no trends in the residuals.

RESULTS

TILLERING.—The three species showed high tiller mortality following shoot removal, regardless of the plants' initial sizes (Fig. 1). This decline in the number of tillers was most pronounced in *A. semiberbis,* where the largest plant size experienced the greatest tiller mortality (86%). Treated plants resumed tillering afterwards, although species differed in the speed of their recovery. Trachypogon *plumosus* recovered most rapidly, whereas *A. semiberbis* recovered most slowly.

In all three species, control plants showed a similar trend of increasing tillering until reaching a maximum number of tillers, followed by a progressive decrease (Fig. 1). Control plants of *A. semiberbis* reached maximum tiller number at the end of the dry season (April), whereas *T. plumosus*

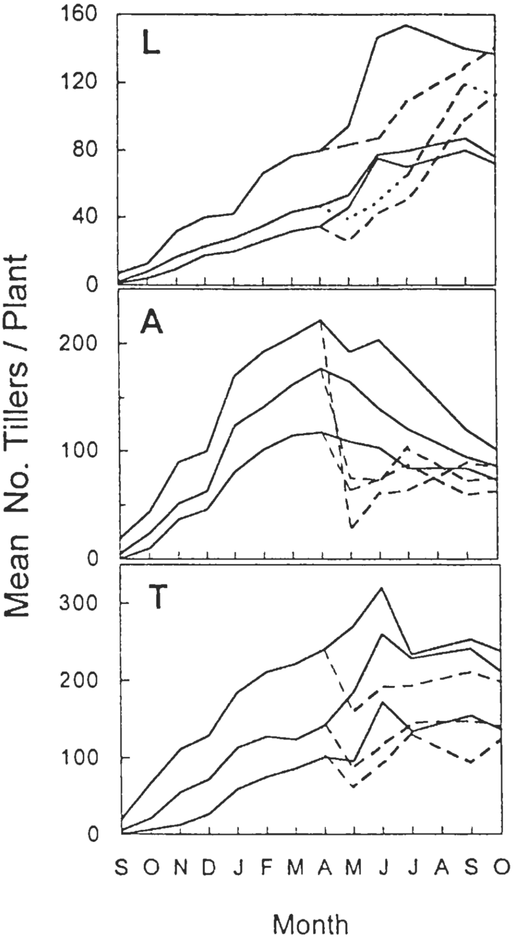

FIGURE 1. Changes in mean plant size (number of tillers) throughout the year (Sept. 1989–Oct. 1990) for control (solid line) and clipped plants (dashed line) in the three initial sizes. L = *Leptocoryphium lanatum*; A = *Andropogon semiberbis*; T = *Trachypogon plumosus*.

and *L. lanatum* reached their maximum sizes in June. The reduction in tiller number was most pronounced in *A. semiberbis* and least pronounced in *L. lanatum*.

In *T. plumosus* and *A. semiberbis*, the final numbers of tillers per plant were not significantly affected either by shoot removal or initial plant size (Table 1). In *L. lanatum*, initial plant size showed significant effects on final plant size ($P < 0.01$), because initial class III produced significantly more tillers per plant than did the other two size classes (Table 1). Less clear is the effect of clipping in *L. lanatum*, since mean final size was just marginally higher in clipped plants (122 tillers) than in the controls (95 tillers; $P < 0.053$, Table 1).

BIOMASS.—There were significant differences on final aerial biomass due to shoot removal only in *T. plumosus* (Table 2), where defoliated plants exhibited almost twice the shoot biomass of control plants at the end of the experiment. Differences due to initial plant size were significant only in *L. lanatum*, in which they were due to differences between size classes I and III (Table 2).

In contrast, total aerial biomass was significantly higher in clipped plants than in control plants for the three species (Table 3). Again, differences in total aerial biomass due to initial plant size were only significant in *L. lanatum*, owing to differences between class I and class III. There was no significant interaction between plant size and shoot removal for any species. *Trachypogon plumosus* had the highest mean total biomass (967 g dry wt./plant), and *L. lanatum* had the lowest mean total biomass (360 g dry wt./plant).

FLOWERING.—In the field, *L. lanatum* usually flowers in May, a few weeks after burning, whereas *T. plumosus* flowers in September and *A. semiberbis* in November, at the end of the rainy season. In the experiment, *L. lanatum* did not flower at all, but *T. plumosus* and *A. semiberbis* flowered within their regular schedules. The analysis of the proportion of flowering tillers (Table 4) showed significant differences between the latter two species, with *T. plumosus* having 44 percent more flowering tillers than *A. semiberbis*.

The fraction of flowering tillers was significantly lower in defoliated plants than in control plants (Table 4). The largest initial plant size flowered significantly more than the smaller initial plant size. There was a significant interaction between species and shoot removal due to the pronounced effect of defoliation on the flowering of *T. plumosus* in contrast to the lack of response in *A. semiberbis*.

DISCUSSION

Fire and grazing, as well as clipping, are causes of tiller mortality (Canales & Silva 1987, Butler & Briske 1988, Simoes & Baruch 1991). In our study, the removal of the aerial biomass at the ground level (common in the case of intense fires) resulted in immediate tiller mortality, reducing the actual size of the living plant in each of the three species. This effect was mediated by plant architecture, species phenology, and the timing of the shoot removal. The species with the deepest lateral meristems and rhizomes (*L. lanatum*) was affected the least by shoot removal, and the species with meri-

TABLE 1. *Comparison of mean final size (number of tillers per plant in October) for defoliated and control plants the three initial size classes (S) within each of the three species. Only initial size in* L. lanatum *render significant differences in mean final size as indicated by different superscripts. Standard errors are in parenthes*

Species	Size class	Treatment Control ($N = 5$)	 Defoliated ($N = 5$)	ANOVA for Size Effect
L. lanatum	I^{a}	72 (15)	113 (18)	
	II^{a}	76 (10)	112 (18)	$F = 5.409, P < 0.01$
	III^{b}	137 (14)	141 (18)	
ANOVA for				
Treatment Effect		$F = 4.128, P < 0.053$		
Interaction S × T		$F = 1.16, P < 0.8567$		
T. plumosus	I	136 (23)	125 (27)	
	II	212 (27)	140 (29)	$F = 1.338, P < 0.28$
	III	238 (24)	198 (37)	
ANOVA for				
Treatment Effect		$F = 0.215, P < 0.65$		
Interaction S × T		$F = 0.55, P < 0.5871$		
A. semiberbis	I	74 (15)	63 (11)	
	II	87 (14)	75 (14)	$F = 1.961, P < 0.16$
	III	102 (11)	86 (19)	
ANOVA for				
Treatment Effect		$F = 0.487, P < 0.49$		
Interaction S × T		$F = 0.06, P < 0.9447$		

TABLE 2. *Mean values of Final Aerial Biomass harvested during October 1990 in the three initial size classes and the two treatments for each species. The numbers in parentheses are the standard errors of the means. Significant differences are indicated with different superscripts.*

Species:		Treatment		
L. lanatum	Size class	Control	Defoliated	ANOVA for Size Effect
Final Aerial Biomass (g)	I^{a}	262 (40.1)	175 (39.7)	
	II^{ab}	230 (51.2)	273 (38.6)	$F = 4.83, P < 0.018$
	III^{b}	376 (42.3)	340 (48.7)	
ANOVA for				
Treatment Effect		$F = 0.66, P < 0.435$		
Interaction S × T		$F = 1.445, P < 0.256$		

Species:		Treatment		
T. plumosus	Initial size	Control^{a}	Defoliated^{b}	ANOVA for Size Effect
Final Aerial Biomass (g)	I	523 (293.0)	678 (176.4)	
	II	419 (90.5)	1064 (297.8)	$F = 0.36, P < 0.70$
	III	493 (165.0)	1380 (135.2)	
ANOVA for				
Treatment Effect		$F = 9.34, P < 0.006$		
Interaction S × T		$F = 0.832, P < 0.449$		

Species		Treatment		
A. semiberbis	Initial size	Control	Defoliated	ANOVA for Size Effect
Final Aerial Biomass (g)	I	388 (118.2)	317 (119.1)	
	II	228 (76.9)	262 (62.4)	$F = 1.14, P < 0.34$
	III	358 (88.7)	358 (38.5)	
ANOVA for				
Treatment Effect		$F = 0.007, P < 0.93$		
Interaction S × T		$F = 0.195, P < 0.824$		

TABLE 3. *Mean values of Total Aerial Biomass (Clipped Aerial Biomass + Final Aerial Biomass) in the three initial size classes and the two treatments for each species. Numbers in parentheses are the standard errors of means. Significant differences are indicated with different superscripts.*

		Treatment		
L. lanatum	Size class	Control^{a}	Defoliated^{b}	ANOVA for Size Effect
Total Aerial Biomass (g)	I^{a}	262 (40.1)	320 (65.2)	
	II^{ab}	230 (51.2)	469 (81.9)	$F = 3.58$, $P < 0.044$
	III^{b}	376 (42.3)	578 (138.5)	
ANOVA for				
Treatment Effect		$F = 8.90$, $P < 0.001$ ✓		
Interaction S × T		$F = 0.96$, $P < 0.395$		
T. plumosus	Initial size	Control^{a}	Defoliated^{b}	ANOVA for Size Effect
Total Aerial Biomass (g)	I	523 (293.0)	1352 (518.9)	
	II	419 (90.5)	2122 (556.7)	$F = 0.36$, $P < 0.70$
	III	493 (165.0)	2298 (349.9)	
ANOVA for				
Treatment Effect		$F = 38.2$, $P < 0.0001$		
Interaction S × T		$F = 0.80$, $P < 0.429$		
A. semiberbis	Initial size	Control^{a}	Defoliated^{b}	ANOVA for Size Effect
Total Aerial Biomass (g)	I	388 (118.2)	812 (137.6)	
	II	228 (76.9)	812 (76.5)	$F = 2.09$, $P < 0.15$
	III	358 (88.7)	1380 (278.5)	
ANOVA for				
Treatment Effect		$F = 33.2$, $P < 0.0001$		
Interaction S × T		$F = 1.05$, $P < 0.369$		

stems above the ground (*A. semiberbis*) was affected the most. In fact, *L. lanatum* possesses rhizomes as deep as 10 cm below the surface, protecting them from the effects of complete shoot removal.

The timing of treatment is an important variable influencing the tillering dynamics of plants (Mullahey *et al.* 1991, Becker *et al.* 1997). Shoots were removed from the plants at the end of April, when *A. semiberbis* had reached their maximum number of tillers. The other two species still continued tillering and reached maximum number of tillers in June (Fig. 1). Shoot removal induced the greatest mortality in species for which production of new tillers had already taken place during the

TABLE 4. *Flowering output as the average fraction of flower tillers per plant for the three initial size classes and the defoliated and control plants. Standard errors are in parentheses. Significant differences are indicated with different superscripts.*

		Treatment			
Species	Size class	Control	Defoliated	ANOVA for Size Effects	ANOVA for Species Effects
T plumosus	I^{a}	0.51 (0.02)	0.19 (0.08)		
	II^{ab}	0.50 (0.05)	0.31 (0.05)		
	III^{b}	0.54 (0.04)	0.29 (0.03)	$F = 3.21$, $P < 0.05$	$F = 15.7$, $P < 0.0003$
A. semiberbis	I^{a}	0.26 (0.04)	0.17 (0.06)		
	II^{ab}	0.24 (0.05)	0.23 (0.03)		
	III^{b}	0.31 (0.04)	0.27 (0.05)		
ANOVA for					
Treatment Effects		$F = 17.0$, $P < 0.0002$			
Interactions					
Spp. × T		$F = 15.6$, $P < 0.0003$			
Spp. × S		$F = 0.78$, $P < 0.464$			
T × S		$F = 1.16$, $P < 0.323$			
Spp. × T × S		$F = 0.36$, $P < 0.698$			

dry season (*A. semiberbis*), but whose tillers were still small due to minimal available moisture. Therefore, the more detrimental effects of fires late in the dry season may be partially due to the phenological state of the population, in addition to high fuel availability (Lacey *et al.* 1982).

The fact that after reaching a certain number of tillers, the tussocks of the control plants undergo a self-thinning process, could be the consequence of tiller competition for light. This response is not only induced by a very high number of tillers, but also may be a consequence of the substantial increase in the aerial biomass and height of the tillers during the rainy season (Raventós & Silva 1988).

In terms of plant biomass, response to defoliation differed among species. *Leptocoryphium lanatum* and *A. semiberbis* compensated for the biomass removed in April, whereas *T. plumosus* overcompensated by producing almost three times more final biomass than the control plants (Table 2). Since the final number of tillers per plant was not affected by defoliation, defoliated *T. plumosus* tillers must have grown significantly more than did tillers of the control plants. This species is dominant largely in Neotropical savannas under annual fires and very low grazing pressure. It has been found to respond negatively to frequent clipping simulating season-long herbivory (Simoes & Baruch 1991). Our results can be interpreted to indicate that this species is better adapted to infrequent shoot removal associated with fire than to frequent herbivory.

We did not measure biomass losses due to decomposition in control plants from May to October. These losses may have influenced the total biomass results of the experiment (final biomass + removed biomass). According to several different estimates discussed by Sarmiento (1984), decomposition accounts for 10 to 50 percent of the annual reduction in standing biomass of savanna grasses, depending on rainfall and other environmental conditions. In the six-month period of our experiment, this loss should not represent more than 50 percent (and very likely no more than one-third) of the biomass (G. Sarmiento, pers. comm.). Such a loss may explain the differences in total biomass in the case of *L. lanatum*, but cannot explain the much larger differences in *T. plumosus* and *A. semiberbis*.

Leptocoryphium lanatum did not flower in the experimental plots. This absence of flowering is not uncommon in some field populations during a given year. We still do not have any explanation for this. Whereas shoot removal reduced significantly the fraction of flowering tillers in *T. plumosus*, flowering of *A. semiberbis* remained unaffected (Table 4). Number of reproductive tillers was also unaltered by thinning of tillers or clones in *Schyzachyrium scoparium* (Briske & Butler 1989). It has been shown that *A. semiberbis* recruits heavily from seeds, in contrast to *T. plumosus* which exhibits an intense clonal recruitment and a low dependence on seed germination (Silva & Ataroff 1985). Consequently, the negative effects of shoot removal by fire may not have any major impact on the population dynamics of the latter species.

Since experimental burning was not feasible, we clipped at ground level to mimic one fire effect (*i.e.*, aerial biomass removal). This removal is, in our opinion, the most important fire effect on adult grass plants as we have shown in previous studies. Other effects, such as direct mortality of meristems by heat and nutrient recycling, were missed. We must emphasize, however, that our results may differ from those of an actual burning. Tiller mortality depends on the intensity of fire, which in turn depends on a series of other factors (Miranda *et al.* 1993). Thus, differences in numbers of tillers between burned and unburned plants may be even lower than in our shoot removal experiment. Furthermore, fire generates a pulse of mineral nutrients to the soil, enhancing tiller growth. Consequently, fire may induce greater compensating responses than experimental shoot removal.

It is interesting to notice that, although differences between the initial size classes were larger in *A. semiberbis* and *T. plumosus* (1, 5, 20) than in *L. lanatum* (1, 3, 7), it was only in the latter species that initial size significantly influenced the three parameters of vegetative growth (number of tillers, final aerial biomass, and total aerial biomass). After a year of growing free from competition, plants reached large sizes with a great variance within each class. Both maximum size and final sizes were well beyond the mean size of the three species commonly observed in the field. Competition is intense among these species growing in the savanna (Raventós & Silva 1988, 1995), and it is playing a role in plant responses to defoliation (Archer & Detling 1984). Therefore, the role of competition within a single defoliation event still needs to be assesed.

The self-thinning of the control tussocks, coupled with the recovery of the experimental plants, resulted in no significant effects of shoot removal on the final numbers of tillers in at least two of the three species. In terms of tillering, the three compensated for the losses due to the shoot removal. The results suggest that *L. lanatum* may exhibit overcompensation of tiller production. The compensating and overcompensating responses in standing biomass allow these species to maintain the photosynthetic gains during the wet season despite the occurrence of fire. The fact that reproductive output of *T. plumosus* under shoot removal was reduced, whereas its vegetative growth was favored, is an indication that fire may be acting as a switch to allocate more energy to vegetative than to reproductive growth. This response would be expected from a clonally reproducing plant that is very successful in frequently burned savannas.

Although inmediate shoot removal effects are strongly negative, it seems clear that these three species are able to recover, not only in numbers of tillers, but also in aerial biomass. Considering the variable intensities of savanna fires and the release of nutrients after burning, we expect the compensating responses to actual fire be greater than the ones resulting from this shoot removal experiment.

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