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Fire and fire exclusion effects on the growth and survival of two savanna grasses

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ABSTRACT

We followed the fate of seedlings and adult plants of two grass species: *Andropogon semiberbis* and *Sporobolus cubensis* in two plots, in a savanna community in western Venezuela. One plot was burnt at the end of the first dry season whereas the other was protected from fire. The results, expressed as probabilities of survival in the case of seedlings and as transition probabilities to different size classes and probabilities of death for adults, were subjected to log linear analysis. We considered the effects on seedling's fate of the following variables: treatment (burnt or excluded), season (dry or wet), and species. In the case of adults, the analysis included the effects of treatment and season, conditional to the initial stage, for each species separately.

Both species suffered appreciable seedling mortality during the dry season when the fire occurred and the growth of adults plants was more impaired in *S. cubensis* than in *A. semiberbis*. Although, both species appear to suffer following fire exclusion, *A. semiberbis* is much more sensitive and its persistence probably depends more strongly on frequent fires, that is the case for *S. cubensis*. Differences between the two species suggest that *A. semiberbis* is a better colonizer under burnt savanna conditions, but that once established, *S. cubensis* resistance to fire protection is higher.

KEYWORDS: population ecology, demography, tropical pastures, tropical savanna, phenology, *Andropogon semiberbis*, *Sporobolus cubensis*.

RÉSUMÉ

Nous avons suivi le devenir de plants jeunes et adultes de deux herbacées (*Andropogon semiberbis* et *Sporobolus cubensis*) sur deux parcelles, dans un peuplement de savane à l'Ouest du Venezuela. L'une des parcelles a été brûlée à la fin de la première saison sèche, alors que la seconde a été protégée du feu. Les résultats, exprimés en termes de taux de survie pour les jeunes plants et, pour les adultes, en termes de probabilités de transition vers des classes de taille différentes, ou de taux de mortalité, ont été soumis à une analyse log-linéaire. Les effets des variables suivantes sur la croissance des jeunes plants ont été pris en compte : traitement (brûlis ou non), saison (sèche ou humide), espèce. Chez les adultes, l'analyse intégrait les effets du traitement et de la saison – conditionnellement au stade initial – pour chaque espèce prise séparément. Les jeunes plants des deux espèces ont un taux de mortalité important au cours de la saison sèche au moment des feux, et la croissance des adultes est plus faible chez *Sporobolus cubensis* que chez *Andropogon semiberbis*. Bien que toutes deux souffrent apparemment de la protection du feu, il semble que *A. semiberbis* soit beaucoup plus sensible et que sa survie soit sans doute plus dépendante de la fréquence du feu que celle de *S. cubensis*. Les différences observées entre les deux espèces suggèrent que *A. semiberbis* est un meilleur colonisateur en savane brûlée mais que, une fois établie, la résistance de *S. cubensis* à la protection du feu est supérieure.

INTRODUCTION

Although fire is considered a prime factor in determining savanna structure and functioning (FROST *et al.*, 1986) there are few studies on the effects of fire on savanna plants (COUTINHO, 1982; LACEY *et al.*, 1982) and on savanna populations (MOTT & ANDREW, 1985; SILVA & CASTRO, 1989). These studies showed that fire, even though it takes place during the dry season, is an important source of mortality, especially for seedlings and small grasses. Several hypotheses have been formulated regarding the effects of fire on savanna structure and on the growth of savanna plants (LACEY *et al.*, 1982; TROLLOPE, 1982, 1984). It has been postulated that savanna grasses would react differently to fires depending on their phenology and architecture (SILVA, 1987). Basal grasses have their meristems below ground and flower in April-May apparently induced by the occurrence of fire (precocious species). Erect grasses have most of their meristems above ground and flower in November at the end of the growth season (late species). Savanna fires are often patchy and commonly take place annually at the end of the dry season, when most of the herbaceous biomass is dry. Our previous research has shown that burning influences the growth and survival of savanna grasses, suggesting that fire and fire exclusion treatments differ in their effects depending on the architectural and phenological type of the species and the size of the plants (CANALES & SILVA, 1987; SILVA & CASTRO, 1989). On this basis, we expect that fire would be more detrimental to erect than to basal grass species, and to seedlings and small plants rather than to large plants (FROST, 1985). We also expect that whereas flowering of a precocious species should be higher after burning than under fire exclusion, these treatments should not affect a late flowering species (SILVA, 1987). Although it is known that accumulation of necromass following exclusion from fire is detrimental to the growth of grasses (VOGL, 1974), there is no information on the differential reaction of grasses with different architecture and phenology, or on the effects of fire exclusion related to plant size in grass species.

Seasonal savannas in western Venezuela are regularly burnt every year during the dry season. In this paper we present the results of a field study conducted for the last four years to compare the growth and survival of a basal-precocious and an erect-late savanna grass species under two conditions: exclusion from fire and under the customary treatment of one annual burning event at the end of dry season.

STUDY AREA

The study was conducted in an experimental area protected from grazing since May 1980, located 10 km West of the city of Barinas, Venezuela (08° 38′ N, 70° 12′ W). Climate is strongly isothermic, with a mean annual temperature of 27°C. In contrast, rainfall is strongly seasonal with a rainy season from May to November and a dry season from January to March. December and April are transitional, some years wet and others dry. Mean annual rainfall is 1,200 mm. The vegetation is an open savanna with sparse trees (*Bowdichia virgilioides*, *Casearia sylvestris*) and several dominant grasses (*Trachypogon plumosus*, *Leptocoryphium lanatum*, etc). More details on savanna composition, phenology, climate and soils can be found in previous papers (SILVA & ATAROFF, 1985; CANALES & SILVA, 1987; SILVA & CASTRO, 1989).

SPECIES

We selected two grass species with very different phenology and architecture. *Sporobolus cubensis* Hitchc., is a precociously blooming species characterized by a basal architecture. Its rhizomes are buried in the upper two cm of the soil and the culms elongate above the ground only to produce the inflorescence. CANALES and SILVA (1987) studied the effects of a dry season fire upon the seasonal growth of adult plants and found that although their meristems are under the soil surface, burning kills many shoots reducing plant size and regrowth capacity. *Andropogon semiberbis* Kunth is a late blooming species with an erect architecture whose rhizomes rise above the ground exposing their lateral meristems. SILVA and CASTRO (1989) followed a cohort for several years under annual dry season burning and showed that fire is an important source of seedling mortality. Additional information on several phenological and reproductive parameters of these two species can be found in SILVA and ATAROFF (1985) and SILVA (1987).

FIELD METHODS

In May 1986 two 20 × 30 m plots were established, each surrounded by a 2 m wide firebreak and divided into 2 m wide strips separated by a narrow path for walking. In each plot, we labelled 500 seedlings of each species along the strips, using iron rods with an aluminium flag and a wire surrounding the plant base. In the same way we labelled 200 plants of *A. semiberbis* classified into three size classes using the number of tillers, as follows: 75 plants with 2 to 10 tillers, 75 plants with 11 to 20 tillers and 50 plants with more than 20 tillers. We also labelled 200 plants of *S. cubensis* classified by size, using four classes of basal diameter as follows: 50 plants 2-5 cm, 50 plants 6-10 cm, 50 plants 11-15 cm, and 50 plants more than 15 cm. Labelled plants were monitored at variable intervals, measuring size and phenological status. Adult plants of *S. cubensis* were monitored from 1986 to May 1988, whereas adults of *A. semiberbis* were monitored from 1986 to February 1989.

In February 1987, a germination experiment for both species was established in each plot, consisting of five randomly distributed replicates of 100 seeds which were set in a regular fashion in a 10 × 10 cm area, the position of each seed marked with a piece of wire. At the end of June, each area was monitored to detect germination.

On 30 March 1987, one of the plots was burnt (from now on referred as plot **B**) and the other was protected from fire (from now on referred as plot **A**). Time of burning was 12:00 hours and we measured the ranges of soil temperature at soil surface and in the upper 5 mm using Omegastick bars (Omega Engineering Inc) using three replicates. Soil surface temperature during the fire was $198°C < t < 232°C$ and in the upper five mm was $101°C < t < 111°C$.

STATISTICAL ANALYSIS

The goal of our statistical analysis is to determine the significance of the treatment effects (fire, season and species) on growth and survival. In the seedling experiment, the data form a 4-way transition frequency table with three explanatory variables: season (*S*, dry or wet), treatment (*T*, burnt or excluded), and species (*E*, *A. semiberbis* or *S. cubensis*) and one response variable, fate (*F*, alive or dead).

In the adult growth experiment, each species was analyzed separately, because the size classes were defined differently for each. For each species, the data form a 4-way transition frequency table with three explanatory variables: treatment (T, burnt or excluded), season (S, wet or dry), and initial state (I, defined by size classes). The response variable was individual fate (F). Four fate categories were defined: "increase" (growing to a larger size class), "stay" (remaining in the same size class), "decrease" (shrinking to a smaller size class), and "die". Structural zeros were included in these tables for cells corresponding to impossible transition of growth out of the largest and shrinkage from the smallest size class. A constant 0.5 was added to all cells prior to analysis.

The analysis of these transitional data uses loglinear models (Bishop *et al.*, 1975; Fingleton, 1984; see Caswell, 1989 for details of demographic applications). In loglinear analysis the transition frequency table is described by a model which gives the logarithm of the cell frequencies as a linear function of the factors defining the table and their interactions. Because we consider only hierarchical models, in which the presence of an interaction implies the presence of all lower order interactions involving those variables, we denote models specifying their highest order interactions. For example, the first line of Appendix 1 gives the model STE, F: this model contains the STE interaction (and thus also ST, SE, TE, S, T, and E) and the main effect F. It excludes all interactions between F and any combination of S, T and E.

The goodness of fit of a loglinear model is measured by the log-likelihood ratio G^2, which is asymptotically distributed as X^2 with degree of freedom equal to the difference between the number of cells in the table and the number of parameters in the model. The significance of a particular interaction is assessed by examining the reduction in G^2 when the interaction is added to a model which excludes that interaction. Thus, for example, comparing the first two lines of Appendix 1 show that adding the SF interaction to the STE, F model reduces G^2 by an insignificant amount; we conclude that the effect of season on fate is not significant. Because the effect of an interaction is always measured relative to a specified model, there is more than one way to measure the significance of any interaction. Thus, we include several different tests of each interaction in Appendix 1.

In the growth experiment, it is also possible to decompose the effect of treatment or season on plant fate into separate components corresponding to each initial state. Thus, when we find, for instance, that treatment (T) has a significant effect on the fate (F) of *S. cubensis* (Appendix 2) we can go farther (Appendix 4) and examine each size class to discover where in the life cycle the effect of fire is greatest.

RESULTS AND DISCUSSION

Germination

Average percent germination for *S. cubensis* in plot **A** was 16.6% and some seedlings were very soon etiolated and attacked by fungus. In plot **B**, germination of *S. cubensis* was extremely low (0.4%). In *A. semiberbis* the percent germination was also very low in plot **B** (2%) as compared to 44% in plot **A**. The low germination registered for both species in the burnt plot is probably the result of low survivorship of recruits because very little canopy developed after the fire, due to low and intermittent rainfall during this period in 1987. Therefore, although fire has been found to encourage recruitment from seeds in some savanna grasses (Mott & Andrew, 1985), it may depend on the precipitation after the fire.

Flowering

S. cubensis in plot **B** produced a very large crop of seeds in May 1987 (46% flowering) in contrast to plot **A** where none flowered. In the flowering season of 1987 (November), only 22% of the labelled *A. semiberbis* adults flowered in plot **A**, whereas in plot **B** this proportion was 87%.

Fire exclusion decreased reproductive output because of very low flowering in *A. semiberbis* and no flowering in *S. cubensis*. Fire as a flowering promotor in precocious species from neotropical savannas has been previously reported (Coutinho, 1982; Sarmiento & Monasterio, 1983), however we expected fire to have no effects on the late flowering species. The fact that fire increased flowering of *A. semiberbis* from 22 to 87% may be due to an indirect effect of fire exclusion. As shown below, accumulated litter reduced growth of shaded plants decreasing their vigor and consequently their reproduction. Other plants besides grasses increase flowering in response to fire in savannas (Coutinho, 1982; Gillon, 1983), and also in other types of tropical and temperate communities (Daubenmire, 1968; Naveh, 1974). The relationships between this response and the flowering phenology of the species has received little attention. Whether this response is due to a positive effect on the vegetative plant vigor or a more direct effect on some hormonal balance of the plant, may depend on the particular species. Coutinho (1982) reported a morphogenetic process of flower induction by fire (pyromorphogenesis) for several species of small undershrubs with xylopodium.

Seedlings

Survivorship of cohorts of seedlings recruited in May 1986 in both plots are shown in Figure 1. The cohorts behaved similarly until burning took place, and

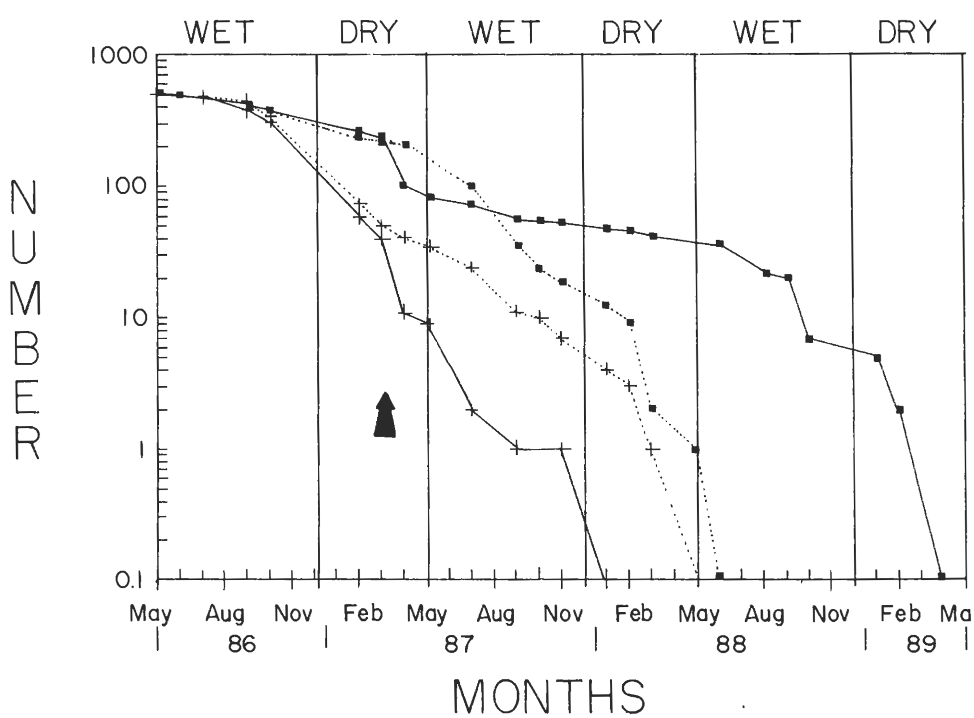

Fig. 1. — Survivorship of cohorts of seedlings from *A. semiberbis* (■) and *S. cubensis* (+). Plot B (——) was burnt in 30 March 1987 (arrow) whereas Plot A (---) was excluded from fire. Lines separating seasons are approximate.

the mortality effects of fire are noticeable in both species. Survival was lower in *S. cubensis* than in *A. semiberbis* during the first dry season in both plots. All four cohorts went extinct before the third year of life, but the only one to survive to the second year was the *A. semiberbis* cohort from plot **B**.

The effects of Treatment, Species and Season on seedlings survival are presented in table I. The corresponding statistical analysis appears in Appendix 1. The main effect of fire exclusion was an increase in survival probability. The main effect of Species was a difference between survival probability of *A. semiberbis* (0.320) and *S. cubensis* (0.076). These two effects were highly significant; the main effect of Season was not significant.

TABLE I. – *Survival probabilities tables.* 1) *Independent effects of state variables* (*Treatment, Season and Species*); 2) *Paired effects;* 3) *Three ways effects. As = A. semiberbis. Sc = S. cubensis.*

1. *Main effect of treatments on seedlings survival*

		% Survival	
Treatment	A	.259	$p < .0001$
	B	.179	
Species	As	.320	$p < .0001$
	Sc	.076	
Season	Dry	.213	$p > .05$
	Wet	.261	

2. *Interaction effects of treatments on seedling survival*

		× Species		
		As	Sc	
Treatment	A	.344	.122	$p < .0001$
	B	.291	.029	

		× Season		
		Dry	Wet	
Treatment	A	.301	.121	$p < .0001$
	B	.127	.580	

		× Species		
		As	Sc	
Season	Dry	.335	.068	$p < .025$
	Wet	.276	.182	

3. *Three way effects of treatments on seedling survival*

		Species As		Species Sc		
		× Season		× Season		
		Dry	Wet	Dry	Wet	
Treatment	A	.45	.11	.11	.20	$p < .01$
	B	.22	.63	.03	.11	

The Treatment × Species interaction shows that fire exclusion affected seedlings of *S. cubensis* more than those of *A. semiberbis*. The Treatment × Season interaction shows that, while fire exclusion improves survival in the dry season, it reduces it in the wet season. Both of these effects are highly significant. The Species × Season interaction, which is more marginally significant, shows that *A. semiberbis* survives better in the dry than in the wet season; the pattern is reversed for *S. cubensis*.

The three-way Treatment × Species × Season interaction is also significant. Its interpretation is aided by figure 1. The experimental fire, late in the dry season, reduces survival in both species. In *A. semiberbis*, survival in the following wet season is higher in the burned than in the protected plot. In *S. cubensis*, by contrast, survival in the burned plot is lower than in the unburned plot. Thus, the two species differ significantly in their seasonal responses to fire exclusion.

ADULTS

Figure 2 shows the survivorship of adult individuals of *A. semiberbis* throughout the three years of study. The exclusion of fire drastically reduced survivorship after the wet season of 1987 (17% in plot A compared to 91% in plot B). This is

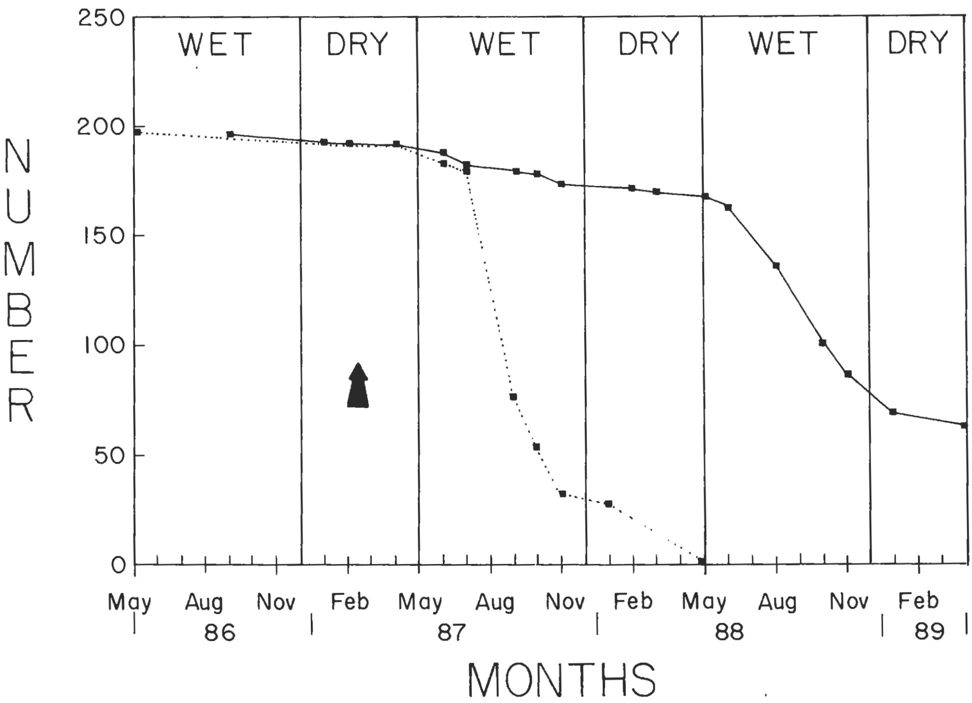

FIG. 2. — Survivorship of *A. semiberbis* adults.
Plot A (---); Plot B (——) The arrow indicates burning.

shown again in 1988, when no fire occurred in plot B and survivorship was only 51%. Adult mortality in *S. cubensis* was so low that we do not include a figure; only 5% in plot A and 4% in plot B during the dry season of 1987, and 6% in plot A and 4% in plot B in the wet season of 1987. During the second dry season (1988) the mortality was again very similar (6 and 7%).

Tables II and III show the transition probabilities by Season, Treatment and the Treatment × Season interaction, for both species. The statistical significance of the differences among these probabilities is documented in the loglinear analysis results (Appendices 2-4). In general, main effects and the interactions were significant, and we turn now to the interpretation of the effects.

TABLE II. — *Main effects of treatment and season, and the treatment × season interaction on transitions of adult* A. semiberbis. *Table entries give the probabilities of transition from each initial state (size class) to four possible fates (increase, stay, decrease, die; see text for definition). The significance of differences among these transition tables is evaluated by the loglinear analyses in appendices* 2 *and* 3. *State* 1 = 2-10 *tillers; State* 2 = 11-20 *tillers; State* 3 ⩾ 20 *tillers. Total initial numbers in each initial state are in parenthesis.*

A) Treatment effects

	Fate	State 1	State 2	State 3	TOTAL
Excluded		(105)	(109)	(159)	(373)
	Increase	0.0	1.8	0.0	0.5
	Stay	16.2	25.7	45.3	31.4
	Decrease	6.7	21.1	45.9	27.6
	Die	77.1	51.4	8.8	40.5
	TOTAL	100.0	100.0	100.0	100.0
Burned		(98)	(65)	(216)	(379)
	Increase	48.0	18.5	0.0	15.6
	Stay	43.9	49.2	38.9	42.0
	Decrease	2.0	26.2	58.8	38.5
	Die	6.1	6.2	2.3	4.0
	TOTAL	100.0	100.0	100.0	100.0

B) Season effects

	Fate	State 1	State 2	State 3	TOTAL
Jan-Apr.		(7)	(50)	(326)	(383)
	Increase	0.0	4.0	0.0	0.5
	Stay	85.7	58.0	44.2	46.7
	Decrease	14.3	34.0	55.8	52.2
	Die	0.0	4.0	0.0	0.5
	TOTAL	100.0	100.0	100.0	100.0
May-Nov.		(196)	(124)	(49)	(369)
	Increase	24.0	9.7	0.0	16.0
	Stay	27.6	25.0	24.5	26.3
	Decrease	4.1	18.5	36.7	13.3
	Die	44.4	46.8	38.8	44.4
	TOTAL	100.0	100.0	100.0	100.0

C) Treatment × Season interaction effects

Treatment	Season	Fate	State 1	State 2	State 3	TOTAL
Excluded	Jan-Apr.		(6)	(41)	(144)	(191)
		Increase	0.0	4.9	0.0	1.0
		Stay	83.3	68.3	50.0	55.0
		Decrease	16.7	24.4	50.0	43.5
		Die	0.0	2.4	0.0	0.5
		TOTAL	100.0	100.0	100.0	100.0
	May-Nov.		(99)	(68)	(15)	(182)
		Increase	0.0	0.0	0.0	0.0
		Stay	12.1	0.0	0.0	6.6
		Decrease	6.1	19.1	6.7	11.0
		Die	81.8	80.0	93.3	82.4
		TOTAL	100.0	100.0	100.0	100.0
Burned	Jan-Apr.		(1)	(9)	(182)	(192)
		Increase	0.0	0.0	0.0	0.0
		Stay	100.0	11.1	39.6	38.5
		Decrease	0.0	77.8	60.4	60.9
		Die	0.0	11.1	0.0	0.5
		TOTAL	100.0	100.0	100.0	100.0
	May-Nov.		(97)	(56)	(34)	(187)
		Increase	48.5	21.4	0.0	31.6
		Stay	43.3	55.4	35.3	45.5
		Decrease	2.1	17.9	50.0	15.5
		Die	6.2	5.4	14.7	7.5
		TOTAL	100.0	100.0	100.0	100.0

The main effect of fire exclusion on *A. semiberbis* is a dramatic increase in mortality and reduction in growth; these effects are greatest in the smallest size classes (table II). The main seasonal effect is an increase in both mortality and growth (especially in the smallest size class) during May-November compared to January-April. The significant Treatment × Season interaction reflects seasonal differences in the response to fire exclusion. The increased mortality and reduced growth due to fire exclusion are apparent in the May-November season, but fire exclusion has little effect during January-April season.

The response of *S. cubensis* is very different (table III). There is little or no mortality response to either fire exclusion or season. The overall seasonal effect is higher growth during October-April, compared to May-November. The effects of fire exclusion on growth are most easily seen by examining each season separately (as suggested by the significance of Treatment × Season interaction). For each size class, fire exclusion reduces growth in the May-November season and has a slight positive impact on growth in November-April. The positive impact of fire exclusion presumably reflects the direct action of fire on meristems, reducing the production of new tillers (CANALES & SILVA, 1987), while the negative impact of exclusion during May-November reflects the increased litter coverage and consequent reduction in light availability.

TABLE III. – *Main effects of Treatment and Season, and the Treatment × Season interaction on transitions of adults* S. cubensis. *Table entries give the probabilities of transition from each initial state (size class) to four possible fates (increase, stay, decrease, die; see text for definition). The significance of differences among these transition tables is evaluated by the loglinear analyses in appendices* 2 *and* 4. *State* 1 = 1-5 *cm; State* 2 = 6-11 *cm; State* 3 = 11-15 *cm; State* 4 ⩾ 15 *cm basal diameter. Total initial numbers in each initial state are in parenthesis.*

A) *Treatment effects*

	Fate	State 1	State 2	State 3	State 4	TOTAL
Excluded		(153)	(111)	(59)	(61)	(373)
	Increase	24.2	11.7	22.0	0.0	16.4
	Stay	66.0	36.0	23.7	52.5	48.7
	Decrease	0.0	49.5	50.8	45.9	29.4
	Die	9.8	2.7	3.4	1.6	5.5
	TOTAL	100.0	100.0	100.0	100.0	100.0
Burned		(59)	(151)	(75)	(62)	(347)
	Increase	10.2	15.2	10.7	0.0	10.7
	Stay	76.3	68.9	58.7	80.6	70.0
	Decrease	0.0	14.6	29.3	19.4	16.1
	Die	13.6	1.3	1.3	0.0	3.2
	TOTAL	100.0	100.0	100.0	100.0	100.0

B) *Season effects*

	Fate	State 1	State 2	State 3	State 4	TOTAL
Oct-Apr.		(138)	(140)	(46)	(51)	(375)
	Increase	29.0	25.7	41.3	0.0	25.3
	Stay	63.0	65.7	52.2	90.2	66.4
	Decrease	0.0	6.4	2.2	7.8	3.7
	Die	8.0	2.1	4.3	2.0	4.5
	TOTAL	100.0	100.0	100.0	100.0	100.0
May-Nov.		(74)	(122)	(88)	(72)	(356)
	Increase	4.1	0.0	2.3	0.0	1.4
	Stay	79.7	42.6	38.6	50.0	50.8
	Decrease	0.0	55.7	58.0	50.0	43.5
	Die	16.2	1.6	1.1	0.0	4.2
	TOTAL	100.0	100.0	100.0	100.0	100.0

C) Treatment × Season interaction effects

Treatment	Season	Fate	State 1	State 2	State 3	State 4	TOTAL
Excluded	Oct-Apr.		(101)	(46)	(24)	(26)	(191)
		Increase	36.6	28.3	54.2	0.0	1.0
		Stay	56.4	67.4	41.7	92.3	61.9
		Decrease	0.0	2.2	0.0	3.8	1.0
		Die	6.9	2.2	4.2	3.8	5.1
		TOTAL	100.0	100.0	100.0	100.0	100.0
	May-Nov.		(52)	(65)	(35)	(35)	(187)
		Increase	0.0	0.0	0.0	0.0	0.0
		Stay	84.6	13.8	11.4	22.9	34.8
		Decrease	0.0	83.1	85.7	77.1	59.4
		Die	15.4	3.1	2.9	0.0	5.9
		TOTAL	100.0	100.0	100.0	100.0	100.0
Burned	Oct-Apr.		(37)	(94)	(22)	(25)	(178)
		Increase	8.1	24.5	27.3	0.0	18.0
		Stay	81.1	64.9	63.6	88.0	71.3
		Decrease	0.0	8.5	4.5	12.0	6.7
		Die	10.8	2.1	4.5	0.0	3.9
		TOTAL	100.0	100.0	100.0	100.0	100.0
	May-Nov.		(22)	(57)	(53)	(37)	(169)
		Increase	13.6	0.0	3.8	3.8	3.0
		Stay	68.2	75.4	56.6	75.7	68.6
		Decrease	0.0	24.6	39.6	24.3	26.0
		Die	18.2	0.0	0.0	0.0	2.4
		TOTAL	100.0	100.0	100.0	100.0	100.0

COMPARISON OF THE TWO SPECIES

Because *S. cubensis* is a basal species with its meristematic tissue underground, we had expected it to suffer less as a direct effect of fire. However, either species suffered appreciable seedling mortality during the dry season when the fire occurred and the growth of adult plants was more impaired in *S. cubensis* than in *A. semiberbis*.

Both *A. semiberbis* and *S. cubensis* appear to suffer following fire exclusion. Similar effects of fire exclusion have been reported in moist tropical grasslands (SCANLAN, 1980), in temperate grasslands (VOGL, 1974; WRIGHT & BAILEY, 1982) and in tropical savannas (MEDINA 1980, 1982). They have been interpreted as the result of inhibition of growth and survival by shading due to accumulated dead biomass. Our results support this interpretation, but in this study we can go further and detect significant differences between the responses of the two species. Both seedlings and adults of *A. semiberbis* suffer greatly increased mortality during the wet season following fire exclusion. Growth of adult plants, specially in the smaller size classes, is also reduced. In *S. cubensis*, by contrast, fire exclusion produces little or not effect on adult mortality. Adult growth of *S. cubensis* is somewhat reduced during the wet season following fire exclusion. Although the different units of measurement used for the two species preclude quantitative comparison, our impression is that this growth reduction is less than that in *A. semiberbis*. Seedlings of *S. cubensis* actually survive better in the more shaded conditions following fire exclusion.

Thus, *A. semiberbis* is much more sensitive to fire exclusion, and its persistence probably depends more strongly on frequent fires, than is the case for *S. cubensis*. Although fire exclusion does reduce growth in *S. cubensis*, adults have a higher probability of surviving until the next fire than do adults of *A. semiberbis*. In another paper (Silva *et al.*, 1991) we used stochastic matrix population models to examine the effect of fire frequency on persistence of *A. semiberbis*; we concluded that a fire frequency less than about 0.85 would lead to extinction. We suspect that if a similar analysis could be conducted for *S. cubensis* it would predict a much lower minimum fire frequency.

The differences between the two species suggest that *A. semiberbis* is a better colonizer under burnt savanna conditions, but that once established, *S. cubensis* resistance to fire protection is higher.

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Appendix 1

Results of loglinear analysis for the correspondent models of the data presented in table I. The explanatory variables are: Season (*S*), Treatment (*T*) and Species (*E*) and the response variable is the Fate (survivorship or death) of the seedling.

Model	Effect	*df*	G^2	$\triangle G^2$	*P*
STE, F		7	310.86		0.0001
STE, SF		6	307.60		0.0001
	Season	1		3.26	>0.05
STE, TF		6	295.05		0.0001
	Treatment	1		15.81	<0.0001
STE, EF		6	153.27		0.0001
	Species	1		157.59	<0.0001
STE, SF		6	307.60		0.0001
STE, TF, SF		5	293.59		0.0001
	Treatment	1		14.01	<0.0001
STE, EF, SF		5	152.25		0.0001
	Species	1		155.35	<0.0001
STE, TF		6	295.05		0.0001
STE, SF, TF		5	293.59		0.0001
	Season	1		1.46	>0.05
STE, EF, TF		5	140.31		0.0001
	Species	1		154.74	<0.0001
STE, EF		6	153.27		0.0001
STE, SF, EF		5	152.25		0.0001
	Season	1		1.02	>0.05
STE, TF, EF		5	140.31		0.0001
	Treatment	1		12.95	<0.0001
STE, TF, SF		5	293.59		0.0001
STE, TF, SF, EF		4	137.86		0.0001
	Species	1		155.73	<0.0001
STE, EF, SF		5	152.25		0.0001
STE, EF, SF, TF		4	137.86		0.0001
	Treatment	1		14.39	<0.0001
STE, EF, TF		5	140.31		0.0001
STE, EF, TF, SF		4	137.86		0.0001
	Season	1		2.45	>0.05
ST, EF, TF, SF		4	137.86		0.0001
ST, ETF, SF		3	125.10		0.0001
	$E \times T$	1		12.76	<0.0001
STE, TSF, EF		3	22.32		0.0001
	$T \times S$	1		115.54	<0.0001
STE, ESF, TF		3	130.57		0.0001
	$E \times S$	1		6.45	<0.025
STE, ETF, TSF, ESF		1	7.02		0.008
STEF		0	0.00		1
	$S \times T \times E$	1		7.02	<0.01

Appendix 2

Results of loglinear analysis for the correspondent models of each of the entire transition matrices with the numerical values of the data presented in tables II and III. Symbols are as follows: I = Initial size; F = fate (increase, stay, decrease and die); T = treatment (burnt, excluded); S = season (dry, wet).

A. semiberbis

Model	Effect	*df*	G^2	$\triangle G^2$	*P*
IST, FI		24	435.38		0.0001
IST, FIS		16	305.42		0.0001
	Season	8		129.96	<0.001
IST, FIT		16	230.24		0.0001
	Treatment	8		205.14	<0.001
IST, FIS, FIT		8	52.86		0.0001
	Season	8		177.38	<0.001
	Treatment	8		252.56	<0.001
FIST		0	0.00		1
	$S \times T$	8		52.86	<0.001

S. cubensis

Model	Effect	*df*	G^2	G^2	*P*
IST, FI		30	328.15		0.0001
IST, FIS		20	116.74		0.0001
	Season	10		211.41	<0.001
IST, FIT		20	255.89		0.0001
	Treatment	10		72.26	<0.001
IST, FIS, FIT		10	49.05		0.0001
	Season	10		206.84	<0.001
	Treatment	10		67.69	<0.001
FIST		0	0.00		1
	$S \times T$	10		49.05	<0.001

Appendix 3

Results of loglinear analysis for the correspondent models of each of the initial state for *A. semiberbis* transition matrices. Symbols are as follows: *F*=fate (increase, stay, decrease and die); *T*=treatment (burnt, excluded); *S*=season (dry, wet).

State 1

Model	Effect	*df*	G^2	ΔG^2	*P*
ST, F		9	167.83		0.0001
ST, FS		6	156.30		0.0001
	Season	3		11.53	<0.01
ST, FT		6	21.95		0.0012
	Treatment	3		145.88	<0.001
ST, FS, FT		3	5.30		0.151
	Season	3		16.65	<0.001
	Treatment	3		151.00	<0.001
FST		0	0.00		1
	$S \times T$	3		5.30	<0.2

State 2

Model	Effect	*df*	G^2	ΔG^2	*P*
ST, F		9	157.45		0.0001
ST, FS		6	118.84		0.0001
	Season	3		38.61	<0.001
ST, FT		6	109.15		0.0001
	Treatment	3		48.30	<0.001
ST, FS, FT		3		45.03	0.0001
	Season	3		64.12	<0.001
	Treatment	3		73.81	<0.001
FST		0	0.00		1
	$S \times T$	3		45.03	<0.001

State 3

Model	Effect	*df*	G^2	ΔG^2	*P*
ST, F		6	110.09		0.0001
ST, FS		4	30.27		0.0001
	Season	2		79.82	<0.001
ST, FT		4	99.14		0.0001
	Treatment	2		10.95	<0.005
ST, FS, FT		2	2.52		0.2836
	Season	2		96.62	<0.001
	Treatment	2		27.75	<0.001
FST		0	0.00		1
	$S \times T$	2		2.52	<0.3

Appendix 4

Results of loglinear analysis for the correspondent models of each of the initial state for *S. cubensis* transition matrices. Symbols are as follows: F=fate (increase, stay, decrease and die); T=treatment (burnt, excluded); S=season (dry, wet).

State 1

Model	Effect	*df*	G^2	G^2	*P*
ST, F		6	40.04		0.0001
ST, FS		4	18.36		0.0011
	Season	2		21.68	<0.001
ST, FT		4	34.74		0.0001
	Treatment	2		5.30	<0.1
ST, FS, FT		2	13.28		0.0013
	Season	2		21.46	<0.001
	Treatment	2		5.08	<0.1
FST		0	0.00		1
	$S \times T$	2		13.28	<0.005

State 2

Model	Effect	*df*	G^2	G^2	*P*
ST, F		9	154.19		0.0001
ST, FS		6	51.22		0.0001
	Season	3		102.97	<0.001
ST, FT		6	114.09		0.0001
	Treatment	3		40.10	<0.001
ST, FS, FT		3	21.85		0.0001
	Season	3		92.24	<0.001
	Treatment	3		29.37	<0.001
FST		0	0.00		1
	$S \times T$	3		21.85	<0.001

State 3

Model	Effect	*df*	G^2	G^2	*P*
ST, F		9	86.34		0.0001
ST, FS		6	25.25		0.0003
	Season	3		61.09	<0.001
ST, FT		6	69.97		0.0001
	Treatment	3		16.37	<0.001
ST, FS, FT		3	5.48		0.1396
	Season	3		64.49	<0.001
	Treatment	3		19.77	<0.001
FST		0	0.00		1
	$S \times T$	3		5.48	<0.2

State 4

Model	Effect	*df*	G^2	$\triangle G^2$	*P*
ST, F		6	45.75		0.0001
ST, FS		4	21.91		0.0002
	Season	2		23.84	<0.001
ST, FT		4	37.10		0.0001
	Treatment	2		8.65	<0.25
ST, FS, FT		2	8.44		0.0147
	Season	2		28.66	<0.001
	Treatment	2		13.47	<0.005
FST		0	0.00		1
	$S \times T$	2		8.44	<0.025