

## Fire, growth and survivorship in a Neotropical savanna grass *Andropogon semiberbis* in Venezuela

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**ABSTRACT.** This study was conducted in a woodland savanna in western Venezuela exclosed from grazing and burnt once a year towards the end of the dry season. Mean annual rainfall is 1500 mm, with a strong seasonality.

Two cohorts of seedlings of *Andropogon semiberbis* were tagged and monitored for up to three years. Several variables such as survivorship, plant size, seedling density, fire damage and distance to the nearest adult were measured or estimated. Two burning experiments to measure survivorship before and after fire, and two seedling-growth experiments to assess competitive interference from adult plants of three grass species were performed.

The highest mortality takes place during the dry season and is due to fire. This decreases as the plants get bigger due to increasing structural complexity of the clump by growth which gives added protection to the meristems. Other mortality factors such as desiccation, uprooting and shading seem to be important during the wet season, when mortality rate is relatively constant. Survivorship during the first year and after three years is strongly correlated to the size attained by the end of the first growing season.

Seedling densities are rather low and do not seem to play any role in survivorship in this population. Adult interference with seedling growth decreases with distance and seems to be due to root competition, although there is a tendency toward increased foliage interference related to the canopy structure of adult plants.

**KEY WORDS:** density, fire, grasses, Neotropics, plant demography, savanna, size, Venezuela.

### INTRODUCTION

In recent years interest has increased in the possible role of life history and traits related to the population dynamics of species in successional processes in communities, especially in tropical savannas subjected to changes in environmental factors (Frost 1985, Frost *et al.* 1985, Lacey *et al.* 1982, Mott & Andrew 1985, Silva 1987). Savanna community changes remain largely unexplained because there is very little knowledge of the population dynamics of savanna plants and their differential susceptibility to fire despite its importance in management (Jones & Mott 1980, Tothill 1971). There is a general belief that burning the savanna favours grasses as against woody plant species (Gillon 1983, Trollope 1982) although some results show that common grass species may be impaired by burning (Canales & Silva 1986, Pressland 1982, Smith

1960). It is probable that differences between grass species in their susceptibility to fire are related to differences in growth form, phenology and demography. These traits are somewhat correlated as shown by Silva & Ataroff (1985) for six codominant grass species from western Venezuela.

A research programme to study the demography of several important grass species from Neotropical savanna communities under field conditions was started to provide information to develop predictive models of community changes in response to changes in environmental factors and disturbance. This paper presents the results of a three-year field study on the demography of *Andropogon semiberbis* (Nees) Kunth, an important grass species from seasonal savanna communities in the Venezuelan Llanos.

#### STUDY SITE AND SPECIES

##### *Study site*

The study was conducted in Hato Palma Sola, a cattle ranch 10 km west of Barinas City (8° 38' N, 70° 12' W) in western Venezuela. Savanna communities occur on hills formed by massive fluvial deposits of late pleistocene age, commonly designated as Qiv. Soils are oxisols, intermediate in texture and very low in nutrients. Drainage is good and the area never gets flooded throughout the wet season. Rainfall is strongly seasonal with May to November being the main wet season while January to March are dry months. Mean annual rainfall is 1700 mm and mean annual temperature 26.5°C.

The community is an open savanna with *Bowdichia virgilioides* H.B.K., *Palicourea rigida* H.B.K and *Casearia sylvestris* Swartz as the more frequent scattered trees. Predominant grass species are *Andropogon semiberbis* (Nees) Kunth, *Axonopus canescens* (Nees & Trin.) Pilger, *Elyonurus adustus* (Trin.) Ekman, *Leptocoryphium lanatum* (H.B.K.) Nees, *Sporobolus cubensis* Hitchc. and *Trachypogon plumosus* (H. & B. ex Willd.) Nees. Fires commonly occur annually during the dry season. For more information on the ecology of these communities see Silva & Sarmiento (1976) and Sarmiento (1983a). A 1 ha experimental plot was fenced in 1979 to exclude cattle and was burned by wildfire in February or March every year from 1979 to 1986.

##### *The species*

*Andropogon semiberbis* is a perennial C4 grass (Medina 1980) commonly found in well-drained savannas in the Orinoco Llanos of Venezuela and Colombia (Sarmiento 1983a). Several important population traits distinguish this species from other savanna grasses (Silva & Ataroff 1985). It grows slowly during the first months of the wet season to reach a peak of growth towards August and flowers in November when the peak of biomass is attained. Adult plants reach up to 2 m tall by the end of the wet season. At this time the plants sprout new tillers which remain small throughout the dry season and restart growth with the onset of rains.

Most adults flower every year producing a large seed crop. Seeds remain dormant in the soil during the dry season and germinate a few days after the onset of the rains. Seed predation occurring before dispersal is very high and accounts for the loss of nearly half the annual seed crop. Seedlings have very superficial roots and remain as a single shoot until the end of the first growing season, when they sprout new tillers.

#### METHODS

##### *The cohorts*

A first cohort formed by 190 plants was labelled in May 1981, immediately after germination, and monitored until May 1983. Plants were labelled using a metallic flag 50 cm in height. Eight flags disappeared during the first three months and the total sample was reduced to 182 individuals. By the end of the second year only 14 individuals had survived and the monitoring was abandoned after the flags were accidentally removed.

A second cohort formed by 500 seedlings was labelled in May 1983, also a few days after germination, in the same area and monitored until May 1986. We demarcated five land strips (20 × 0.2 m) and labelled all seedlings found up to 500. Each seedling was labelled using a metallic flag as above and was encircled using a fine wire. During the first year, seven individuals disappeared and the total size of the cohort was reduced to 493 plants. In addition to survivorship, information was gathered on plant size, seedling density, fire damage and distance to nearest adult grass plant irrespective of species.

In August 1981 plant size was measured as height of the top leaf base and simultaneously 12 seedlings randomly chosen from the neighbourhood were used to correlate height to total dry weight. In December 1981 and thereafter, size was measured as number of tillers per plant. The number of seedlings in a 3 cm radius of each labelled seedling were counted to determine density. Fire damage was assessed using a scale of 1-3: (1) minor damage: only leaf tips burnt; (2) medium damage: all leaves burnt, shoot bases intact; (3) high damage: shoot bases burnt, only a stump remains. Independence of survivorship from growth and from fire damage was tested by means of the G-test (Sokal & Rohlf 1969). Survivorship from the two cohorts was compared using the G-test, the logrank test and the Gehan-Wilcoxon test (Pyke & Thompson 1986).

##### *The fire experiments*

Two experiments were set up near the experimental plot. The first consisted of two 10 × 10 plots protected by a 2 m wide firebreak. On 20 December 1983, a sample of 190 seedlings was randomly chosen and tagged in each plot. Survivorship was monitored on 12 April 1984, after which one of the plots was intentionally burnt. Survivorship was again monitored on 29 May 1984. A second experiment was set up on 14 December 1984, in two new plots with

150 tagged seedlings in each plot. One of the plots was burnt on 21 March 1985. Survivorship was monitored on 14 May 1985.

In April 1984, living plants were identifiable since some green foliage still remained. But the following dry season was very severe and all foliage was dead in March not allowing detection of surviving plants. Therefore, survivorship before fire was not checked in the second experiment. Survivorship was compared in the two treatments using the G-test.

#### *Adult-seedling interference experiments*

Seedlings which had germinated near the experimental plot by May 1984 were randomly transplanted during the first week of July 1984 as follows:

- at three distances (0-1, 5-7 and 14-16 cm) from the base of adult individuals of *Andropogon semiberbis*, *Elyonurus adustus* and *Leptocoryphium lanatum* all in the same compass direction (SW). This experiment had five replicates.

- at 0-1 cm from the base of adult plants of the three species, but keeping apart the roots or the foliage or both the roots and the foliage as explained below. The 0-1 cm group of the other experiment was used as control. Root separation was achieved by burying an iron sheet 18 cm wide and 25 cm deep

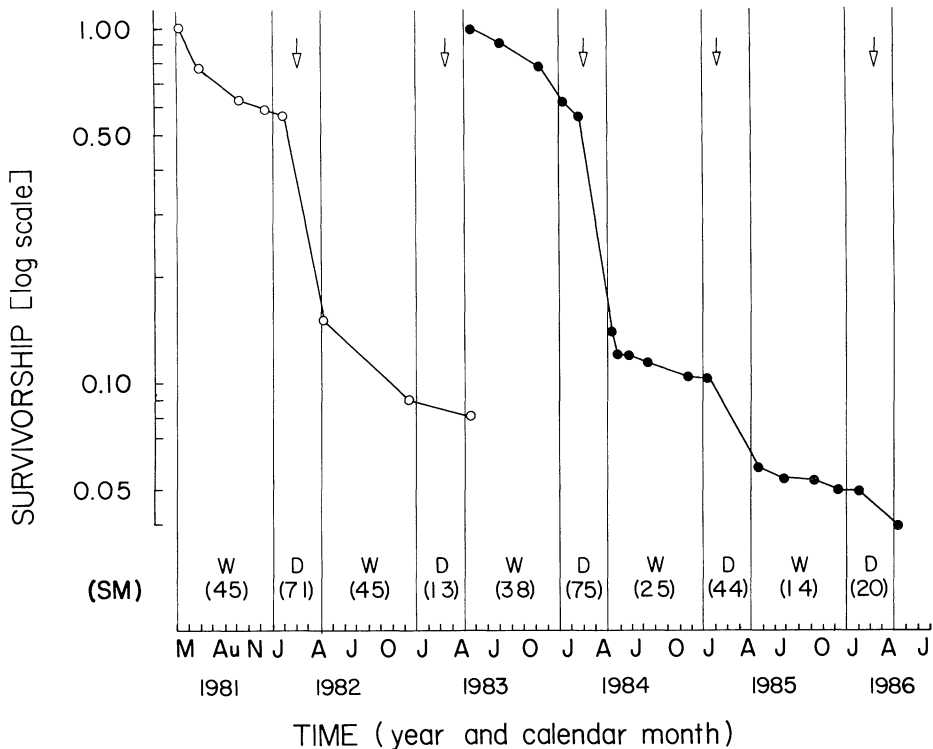


Figure 1. Survivorship of the two seedling cohorts: 1, N=190 (○); 2, N=500 (●). Arrows indicate the occurrence of fire. W = wet season; D = dry season. Within parenthesis the rate of seasonal mortality (SM) as percentages.

at the base of the adult plant prior to transplanting. Foliage separation was achieved by bending the adult plant foliage in the opposite direction to the transplant by means of wires. This experiment also had five replicates.

Both experiments were conducted next to the experimental plot. All other plants in a 30 cm radius from the adult experimental plant had been removed previously and the experiment was periodically checked to maintain this area free of new plants. This removal was carefully made by mechanical means and was limited to extracting rhizomes and stems from the top soil. In both experiments dead seedlings were replaced until 16 August using, as replacements, nearby seedlings about the same size as the experimental seedlings. A total of 33 replacements (30% of the total number) were performed. The proportion of replacements was not different for the different treatments, with the exception of the foliage exclusion with a total of 12 replacements, six of which were under *Leptocoryphium lanatum*. This should be considered as a possible bias for the results of this particular set. The seedlings grew until 11 January 1985, when all were cropped. In the laboratory they were washed to remove the soil, separated into below and above ground parts and oven dried to constant weight. Total, above-ground, and below-ground biomass as well as shoot: root quotients for the different treatments and species were compared using a two-way analysis of variance with replicates. A Tukey test was used to compare means.

## RESULTS

### *Survivorship*

Survivorship curves of Cohorts 1 and 2 (Figure 1) show the same pattern despite differences in the values of seasonal mortality. At the end of the first season of growth (December) survivorship in both cohorts was not statistically different ( $G = 0.49$ ) despite the fact that the shape of the curves during that period was significantly different ( $LR = 12.46$ ;  $Z = 4.38$ ,  $P < 0.001$ ). Survivorship to the second dry season was also different in both cohorts ( $G = 7.34$ ;  $P < 0.01$ ).

The statistical comparison of the curves (for the first two years) renders contradictory results. With the logrank test the two curves are not significantly different ( $LR = 3.28$ ) but with the Gehan-Wilcoxon test the differences are very significant ( $Z = 4.51$ ,  $P < 0.01$ ). Survivorship to the second year is also not significantly different in the two cohorts ( $G = 1.22$ ). These statistical disagreements are not uncommon (Pyke & Thompson 1986). Mortality during dry seasons is higher than during wet seasons and is particularly high in the first dry season of the seedling's life.

In Cohort 2 it is apparent that mortality increased slightly when passing from the first wet season to the first dry season up to the middle of February, when the savanna was burnt. After burning, the seedlings did not show any growth until the rains started in late April. Of those alive before the fire, 74%

were dead by May 1984. The second and third wet seasons started with high mortalities (May–June), which decreased very much (1984) or became nil (1985). Mortality during the second dry season was significantly lower than during the first dry season ( $G = 22.45$ ,  $P < 0.001$ ).

Seedling predation was very minor and could not be considered a cause of death. Other mortality factors were desiccation, uprooting by soil surface erosion and shading. The first two of these were about equal and probably the two most important causes of mortality during the first part of the wet season. When seedlings were found dead, dry and without marked etiolation, it was concluded that desiccation was the cause of death. Many seedlings were found dying or dead partially or totally uprooted by erosion. This was intense during the first wet season. Many seedlings were uprooted or had their roots exposed and died by desiccation. This mechanical mortality factor operated only during the first growing season. Etiolation followed by death was less important and apparently acted only towards the end of the wet season, when the plants resprout. All these mortality factors are very difficult to quantify and so these results are estimates.

#### *Fire as a mortality factor*

The degree of fire damage to seedlings was evaluated after the February 1984 fire. Almost all (92%) of the 119 seedlings in category 3 (high damage) died, 70% of the 119 seedlings in category 2 (medium damage) also died, compared to only 40% mortality of the 30 seedlings in category 1 (minor damage). These differences were very significant ( $G = 39.07$ ,  $P < 0.001$ ).

The results of the fire experiments are presented in Table 1. In Experiment 1, on both plots, half the individuals had survived the dry season until April. The

Table 1. Results of two field experiments to study the effect of burning on the survivorship of *Andropogon semiberbis* seedlings. In Experiment 1, burning took place on 12 April 1984. In Experiment 2, burning took place on 21 March 1985. Survivorship is conditional; 1 = 100% survivorship.

<i>Experiment 1</i>				
Plot		December 1983	April 1984	May 1984
Burnt:	Number	190	93	9
	Survivorship	1	0.40	0.09
Unburnt:	Number	190	103	92
	Survivorship	1	0.54	0.89
<i>Experiment 2</i>				
Plot		December 1984	May 1985	November 1985
Burnt:	Number	148	42	41
	Survivorship	1	0.28	0.97
Unburnt:	Number	150	127	103
	Survivorship	1	0.84	0.81

effect of fire is shown clearly in the survivorship on both plots in May 1984. In Experiment 2, survivorship at the beginning of the rainy season, in May 1985, was much higher in the unburnt than in the burnt plot. In both experiments the differences were very significant ( $G_1 = 142.40$ ;  $G_2 = 102.60$ ,  $P < 0.001$ ). The higher survivorship after the 1985 fire compared to the 1984 one, is probably due to this area not being burnt in 1983 and, therefore, fire intensity in 1984 was greater than in 1985. In order to test the possibility that overshadowing by remaining vegetation in the protected plot constituted a significant contribution to mortality during the growing season, both plots were re-censused at the end of November 1985. The results showed (Table 1) that survivorship to the wet season was significantly higher in the burnt plot than in the unburnt plot ( $G = 9.08$ ,  $P < 0.01$ ).

#### *Growth, density and survivorship*

The possible effects of differences in growth rates on survivorship in Cohort 2 were appraised by comparing seedling height attained by the middle of the first growing season with survivorship over the whole season (Table 2). The figures show clearly that survivorship is significantly related to size ( $G = 10.72$ ;  $P < 0.025$ ). Furthermore, height and total biomass of seedlings, measured in August, were significantly correlated ( $r = 0.86$ ,  $P < 0.001$ ). At the end of October, the seedlings had completed the development of their first initial shoot and the highest shoots were in the 30–40 mm class. At this time, they start to grow new shoots from the short internodes in the rhizome.

In Table 3, the numbers of plants with and without new tillers by November 1983, and survivors in each class to February 1984 (before the fire), to May

Table 2. Relationship between height of seedlings by the middle of the first growing season and survivorship by the end of the first growing season.

Height class (mm)	Number of seedlings	Survivorship (proportion)
0–10	127	0.42
11–20	228	0.73
21–30	85	0.84
> 30	25	0.96

Table 3. Proportion of plants tillering by the end of the wet season (November 1983) and survivorship after two months of drought (February 1984), after the first fire (May 1984) and after three years (May 1986).

	Number of plants in November 1983	Survivorship		
		February 1984	May 1984	May 1986
Tillering	35	0.97	0.34	0.17
Not tillering	349	0.65	0.17	0.05
Total	384	0.68	0.18	0.07

1984 (after the fire), and to May 1986 are presented. Only 9% of the cohort sprouted (one to three new shoots) by the end of the first season of growth, but 97% of these survived to 16 February (after two months of drought), compared to 65% survivorship in the other group. This difference is significant ( $G = 20.80$ ,  $P < 0.001$ ). The differences between the two groups in survivorship after the fire are not significant. However, for May 1986, there were three times more survivors within the group which sprouted new shoots in November 1983 than within the group that did not, and this difference is significant ( $G = 5.55$ ,  $P < 0.05$ ). Flowering frequency for the end of the third wet season was 48%, and there were no significant differences between the two groups.

The mean density was  $0.06$  seedlings  $\text{cm}^{-2}$  with a maximum value of  $0.21$  seedlings  $\text{cm}^{-2}$ . We classified seedlings in density classes from  $0.03$  to  $0.21$  seedlings  $\text{cm}^{-2}$  and found that seedling densities and survivorship are independent ( $G = 2.52$ ).

#### *Interference from adults*

The experiments gave significant positive linear correlations between distance from adult and seedling biomass as shown in Figure 2. Correlation coefficients are all significant at  $P < 0.01$ . With adults of *Leptocoryphium lanatum* ( $r = 0.90$ ) and *Andropogon semiberbis* ( $r = 0.96$ ), the slopes are not different, but seedling biomass was higher with the former. With *Elyonurus adustus*, the effect of distance is less important than in the other two cases.

It is the separation of roots, not foliage, which increases final total biomass per seedling (Figure 3). A two-way analysis of variance of log-transformed

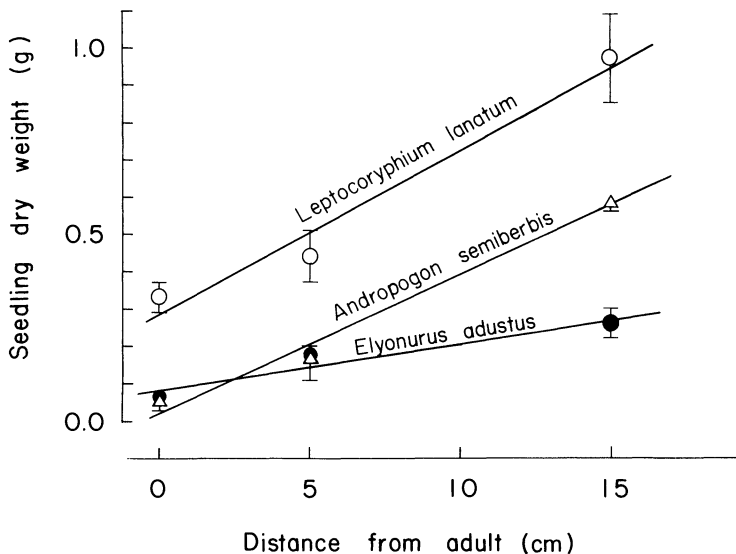


Figure 2. Seedling total biomass as a function of distance from adult. Lines are fitted linear regressions ( $P < 0.01$ ). Vertical lines are standard errors.



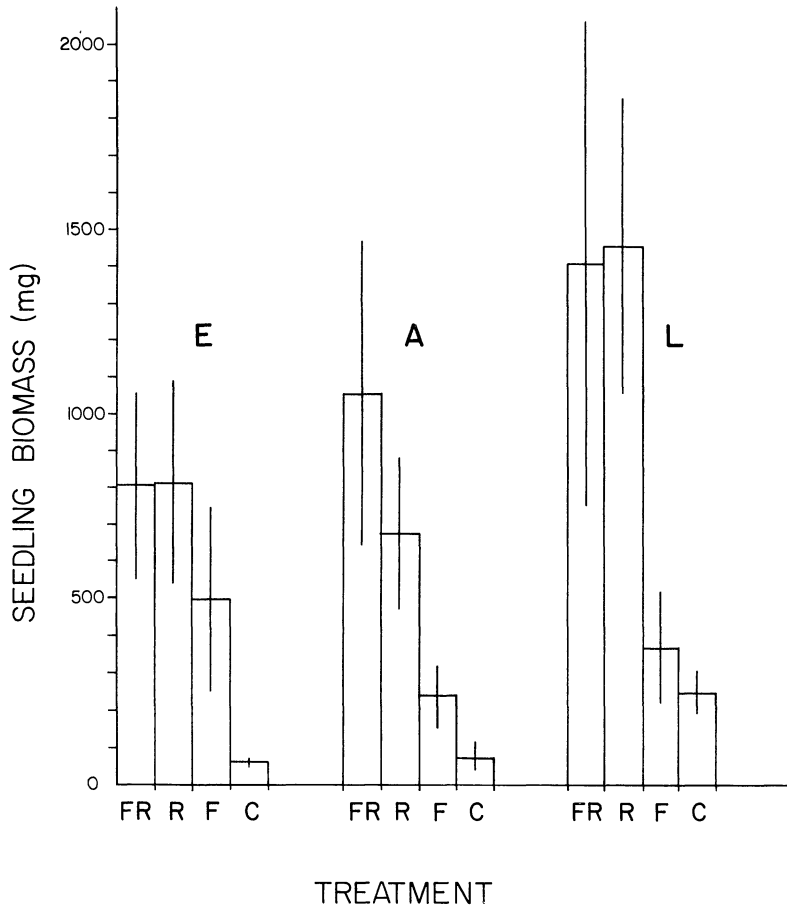


Figure 3. Seedling total biomass after a six-month experiment growing close to an adult plant (A = *Andropogon semiberbis*; E = *Elyonurus adustus*; L = *Leptocoryphium lanatum*) under different treatments: FR = Foliage and roots separated; R = Roots separated; F = Foliage separated; C = control.

values rendered significant differences between modes of separation and between species but no significant interaction between species and modes of separation ( $P < 0.01$ ). Mean seedling total biomass was significantly higher than the control in the root and the root and foliage separation cases ( $P < 0.01$ ). Total biomass of seedlings was significantly higher in the treatments with *L. lanatum* compared to the treatments with *E. adustus* and *A. semiberbis* ( $P < 0.01$ ).

The same results were obtained for aerial biomass and shoot:root quotients of seedlings (Table 4). This last result is important because seedlings showed differential biomass allocation under the different competitive treatments and with different species. Mean shoot:root quotients were significantly less in the control groups than in the treated groups. Furthermore, root and root-foliage separation treatments resulted in higher shoot:root ratios than foliage separation and control.

Table 4. Mean values of above-ground biomass and shoot:root quotients of *A. semiberbis* seedlings growing close to adults of three species under experimental separation of foliage, roots or both. The values in parentheses are standard errors.

Accompanying species	Mode of separation	Mean above-ground biomass (mg)	Shoot:root quotient
<i>Andropogon semiberbis</i>	none (control)	97 (37.0)	4.3 (0.79)
	foliage	204 (72.6)	5.7 (0.81)
	roots	626 (197.7)	11.1 (2.14)
	foliage + roots	987 (394.1)	13.6 (2.13)
<i>Elyonurus adustys</i>	non (control)	51 (3.8)	4.8 (0.92)
	foliage	463 (243.5)	11.5 (2.21)
	roots	751 (266.4)	13.3 (3.19)
	foliage + roots	765 (245.8)	19.0 (2.12)
<i>Leptocoryphium lanatum</i>	none (control)	220 (52.3)	7.8 (1.69)
	foliage	340 (139.8)	10.2 (1.11)
	roots	1401 (386.0)	23.8 (1.47)
	foliage + roots	1356 (628.0)	21.9 (2.85)

### Flowering

Only one plant flowered (for the first time) at the end of the second season of growth, with three floral stems. At the end of the third growth season (December 1985) the cohort was reduced to 25 individuals, 12 of which flowered, most of them producing one single floral stem. Two individuals produced five and seven floral stems and they were among the five larger individuals of the cohort, but there was no significant correlation between size and number of flowering stems in December 1985.

### DISCUSSION

Differences in seasonal survivorship among the cohorts suggest that environmental fluctuations influence the demographic behaviour of annual cohorts. However, the general pattern is very similar. Mortality was significantly higher during the dry season than during the growing season for the first three years in the life of a cohort. This mortality was mostly due to fire. Previous studies have shown that the seedling stage is the 'bottle neck' of many plant populations (Grubb 1977), that seedlings die mostly during the growing season and that this mortality is density dependent (Harper 1977, Sarukhan & Harper 1973). We found that in this savanna, *Andropogon semiberbis* seedling density is generally low and mortality during the growing season is independent of seedling density. This could also be true for the other perennial grass species from this community since their seedlings are generally sparse (Silva & Ataroff 1985). The only cases of seedlings forming dense patches are of ephemeral species (i.e. *Eragrostis maypurensis*) which grow in disturbed or empty places (Monasterio & Sarmiento 1976), but there is no data on their survivorship.

In contrast, competitive interference of seedlings may come from adult

plants. The experiments at variable distances and with foliage and root separation showed that proximity of adult plants from three species (including *A. semiberbis*) resulted in considerable interference to seedling growth. Root competition seems to be more important than competition for light, which is related to the canopy structure of the adult plant. The removal of aerial dry biomass by fire diminishes the interference of adult canopies during the first months of the growing season, but probably increases root interference, since fire stimulates grass growth (San Jose & Medina 1975). The effects of root separation were more important than foliage exclusion and these seedlings were five to seven times taller than the average size of the control group. The effects of root exclusion were more important with *Leptocoryphium lanatum* than with the other two species, not only on the total plant biomass but also in the shoot: root quotient. Under root and foliage-competitive interference from adults, the seedlings grew less and invested more in root than in shoot growth. This effect depends on the species of the adult plants.

Similar importance of root competition was reported for *Panicum maximum* var. *trichoglume* seedlings growing with adult plants of *Heteropogon contortus* (Cook & Ratcliff 1984). Nutrient deficiency as a result of low available nutrients and root-competitive interference by adult plants seems to be responsible for the diminished growth of seedlings (Cook 1985). This is probably a good explanation for the results presented here, given the oligotrophic nature of these savannas.

If competitive interference from adult plants results in less growth we would expect this to be reflected in lower survivorship of seedlings. However, when we used data from Cohort 2 to compare survivorship by the end of the growing season to distance from the nearest neighbour we found these to be independent.

Fire damage is related to the fact that *A. semiberbis* plants, have their rhizomes and therefore their meristems up to 2 cm above the ground, in contrast to most grass species with underground rhizomes. If a fire were intense enough and of long enough duration, it would destroy all the meristems and the plant would not be able to regrow. The intensity of fire damage is significantly correlated to mortality. On the other hand, it became evident that further growth of plant-survivors of fire resulted in structural complexity of the clump, which did not allow fire to kill the inner shoot bases. So, more meristems survived and the plants were able to regrow. This is reflected in the decreasing fire mortality from the first to the third dry season. However, after the first wet season the plants probably were still too small for this to have any effect. This may be why no significant dependence between size and survivorship to the first fire was found.

We do not have data on the effect of season of burning on *A. semiberbis*, but it is clear that during the late dry season, the plants are not at their peak of physiological activity. The mortality effect of late dry season fire on *A. semiberbis* shows that plants do not necessarily need to be physiologically active to be killed by fire as suggested by Gillon (1983) and Trollope (1982) and that

fire may seriously impair some grass populations. On the other hand, our burning experiments allowed us to estimate mortality by overshading. Since mortality during the wet season in the unburnt plot was significantly higher than in the burnt plot, we inferred that overshading should be an important cause of mortality in savanna communities protected from fire.

Growth during the first wet season is significantly correlated to survivorship of *A. semiberbis*, and the size reached by the end of this season is significantly correlated to survivorship during the first three years of life. This implies surviving three late dry season fires. Size rather than age, has been pointed out as the major determinant of survivorship and fecundity in plant populations (Caswell 1986, Werner 1975), and significant correlations have been reported between size and survivorship in herbaceous (Newell *et al.* 1981, Solbrig *et al.* 1980) and tree species (Piñero *et al.* 1984). For *Viola sororia* it has been shown that size differences are responsible for differential survivorship and are mostly due to environmental rather than genetic factors. These environmental factors may be related to germination sites (Solbrig 1981). Since *A. semiberbis* seeds are dispersed by wind, the probabilities of surviving have a large stochastic component. Furthermore, our observations show that larger size gives the plant a higher probability of survival by different mechanisms throughout the year: during the first months of life by better anchoring against erosion; and in the second and third years of life, by protecting against fire by making clumps structurally more complex and also by the accumulation of sediments which help to bury the rhizomes.

There is almost no information on the life cycles of grassland and savanna plants. It is probable that, besides a high diversity in phenological types (Sarmiento 1983b, Sarmiento & Monasterio 1983), Neotropical savannas are also diverse in demographic types from a short cycle, high seed-relying to a very long cycle and low seed-relying grass species and these differences may be important in successional changes, particularly when reacting to changes in the prevailing patterns of disturbance and stress (Frost *et al.* 1985, Lacey *et al.* 1982). Based on the short juvenile period (three years?) and the very high annual seed crop and estimated annual recruitment (Silva & Ataroff 1985), we suggest that *A. semiberbis* is a short cycle perennial in contrast to other savanna grasses such as *Trachypogon plumosus* which are probably very long lived.

We conclude that in this population, fire is the most important source of mortality, even though it takes place during the dry season when *A. semiberbis* plants are apparently resting. Seedling competition does not play any role since densities are low, but seedling growth is impaired by the proximity of adult grasses. Root competition, possibly for nutrients, seems responsible for this. The adult interference not only diminishes seedling growth but also induces a decrease in the shoot:root quotient. Survivorship is dependent on growth and we detected some indirect ways by which larger plants may survive fire. These results allow the interpretation that selective pressures other than fire may be responsible for those traits which allow savanna grasses to persist within a

certain range of fire frequencies, intensities and times of occurrence. If this is so, the evolutionary role of fire in savanna communities would have to be rediscussed.

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