

## **Phenology, seed crop and germination of coexisting grass species from a tropical savanna in Western Venezuela**

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### **ABSTRACT**

1) Six coexisting grass species from a seasonal savanna in Western Venezuela were studied during a 20-month period. In the field, measurements were made of phenology, increase in aerial biomass, diaspore production, seed number and germination. Laboratory measurements were made of the fraction of diaspores carrying a caryopsis, caryopsis viability and germination after dispersal.

2) Three species flowered precociously by the beginning of the rainy season and also showed similar patterns of leaf and shoot production. The other three species flowered at different times (early, intermediate and late during the wet season) and showed different patterns of shoot production

3) Precocious species produced less diaspores per plant and per dry weight than did later bloomers with the exception of *Trachypogon plumosus* (a late bloomer with a low reproductive output but a high vegetative spread). Seeds produced by precocious species germinated as soon as they reached wet ground, but the seeds from the other species remained dormant in the soil until the start of the following rainy season. Thus, all seeds germinated during the first months of the rainy season.

KEY-WORDS: *Savanna - Grasses - Phenology - Seed crop - Germination.*

### **RÉSUMÉ**

1) Pendant une période de 20 mois nous avons étudié six espèces de graminées qui coexistent dans une savane saisonnière du Venezuela. Dans son milieu naturel nous avons suivi la phénologie, la production de diaspores, la quantité de graines et leur germination. Au laboratoire nous avons déterminé la proportion de diaspores qui portent une caryopse, ainsi que la viabilité de ces caryopses et leur germination après dispersion.

2) Trois espèces ont une floraison précoce, juste après les premières pluies de la saison pluvieuse, et montrent les mêmes rythmes de production du feuillage et des tiges. Les trois autres espèces fleurissent pendant la saison pluvieuse, une au commencement, une autre au milieu et la dernière à la fin. De plus, elles montrent différents rythmes de production de tiges.

3) Mis à part *Trachypogon plumosus* qui a un nombre très réduit de caryopses et une importante propagation végétative, les espèces produisent d'autant plus de diaspores (par plante et par poids sec) qu'elles ont une floraison plus tardive. Les caryopses des espèces précoces germent vite sur un substrat humide. Au contraire, celles des autres espèces ont une longue période de latence qui dure jusqu'au commencement de la saison des pluies suivante. En conséquence, les caryopses de toutes ces espèces germent en même temps durant le premier mois de la saison pluvieuse.

MOTS-CLÉS : *Savane - Graminées - Phénologie - Semence - Germination.*

## INTRODUCTION

After twenty years of ecological research on the tropical savannas of Venezuela, there is a sizeable amount of information on several aspects of the structure and functioning of this tropical ecosystem. A recent review is given by SARMIENTO (1983 *a*). However, very little is known regarding the population ecology of common species of savanna plants, both grasses and trees. Most of the available information at the population level concerns phenology (MONASTERIO & SARMIENTO, 1976; RAMIA, 1977, 1978). There are a few works on the population biology of trees (ATAROFF, 1975; XENA *et al.*, 1980; RAMIREZ & ARROYO, 1980) and on the architecture and growth dynamics of grasses (ATAROFF, 1980). This lack of population studies of savanna plant species limits our understanding of savanna communities in both the New and the Old world; particularly critical is the lack of data on the dominant grass species which are responsible for most of the primary production in these systems (SARMIENTO & MONASTERIO, 1983; SARMIENTO, 1978; CESAR, 1971; CESAR & MENAUT, 1976; LAMOTTE, 1975).

Savanna communities are relatively rich in species and within one community several grass species are important contributors to the total biomass (SARMIENTO & MONASTERIO, 1971). These codominant species are always perennial grasses, very similar in life form and general phenology, suggesting great niche overlap. Furthermore, reported differences in vertical distribution of biomass (SARMIENTO, 1978) suggest further differentiation among coexisting species regarding plant architecture and tiller formation dynamics as reported for less diverse grassland communities (MCKENDRIK *et al.*, 1975). Moreover, although all these species are reported flowering every year, information is lacking on their reproductive dynamics. And in a similar way with other grassland and savanna areas, there is an unsubstantiated belief that vegetative reproduction is the common reproductive strategy of dominant grasses, while sexual reproduction is rare (BERG, 1972; MCKENDRIK *et al.*, 1975).

SARMIENTO (1983 *b*), distinguished precocious, early, intermediate and late flowering phenological types among dominant grass species in tropical seasonal savanna communities. If grass species from tropical savannas are flowering at different times during their growing season as shown by SARMIENTO (1978), they probably differ along other axes of their "regeneration niche" (GRUBB, 1977). For instance, late bloomers produce their seeds when the wet season is advanced, and it might therefore be expected that these species would exhibit dormancy in order to enable them to survive until the next wet season. Dormancy should be lacking in early produced seeds and these should germinate as soon as they are in contact with wet ground, in order to maximize the length of their first growing season. Furthermore, if late-produced seeds have to wait several months before becoming seedlings there would be an added mortality risk for them when compared to the seed crop of early blooming species coexisting in the same community. Late bloomers would be expected to compensate for this added mortality by producing a larger annual seed crop than early blooming species.

In this paper we present preliminary results from a 20-month field study on the reproductive ecology of six perennial grass species which coexist in a seasonal savanna in western Venezuela.

## MATERIALS AND METHODS

Six species were selected for this study: *Elyonurus adustus* (Trin.) Ekman, *Sporobolus cubensis* Hitchc., *Leptocoryphium lanatum* (H. B. K.) Nees, *Axonopus canescens* (Trin.) Pilger, *Andropogon semiberbis* (Nees) Kunth., and *Trachypogon plumosus* (H. and b. ex. Willd.) Nees. These species are perennials usually found as codominant in the herbaceous stratum of seasonal savanna communities from the Western Llanos of Venezuela (SILVA & SARMIENTO, 1976).

The study area is a typical seasonal savanna on the Andean piedmont hills of Barinas State, located 10 km west of the city of Barinas (08 28' N-70 12' W). Mean annual temperature is 27° C, mean annual rainfall 1,500 mm. Temperature varies little throughout the year, but rainfall is markedly seasonal, with four to five months with little or no rain (December to April) and seven to eight months of wet season (April to November). Climatically, the area belongs to the Llanos Region of Venezuela (MONASTERIO, 1970).

Dominance by grass species appears to be patchy (ATAROFF, 1983). Cover was measured by random points. It was found that *Elyonurus adustus* and *Trachypogon plumosus* were the two most important species, but their cover values varied widely between 20 and 80 %. At a second ranking level were *Leptocoryphium lanatum*, *Andropogon semiberbis*, *Sporobolus cubensis* and *Axonopus canescens*, whose cover values varied widely between 0 and 40 %.

Twenty healthy looking adult plants of each of the six species were selected and marked, and new tiller formation, new leaf production, reproductive growth and aerial biomass growth were monitored. The aim was to check if the populations were partitioning flowering time as described by SARMIENTO (1983) for other populations of these species, and also to explore further differentiation in patterns of vegetative growth.

Monitoring of seed germination in the field was difficult because of the complex patterns of seed spread and the numbers of seeds produced. Because some of the species produce scores of seeds and very many seedlings, whereas others produce fewer seeds and only very few seedlings, several sizes of plots were compared in order to select a size which provided a compromise between the excessive work involved in monitoring the abundant-seeding species and the need to detect germination of the scarcely-seeding species. After tests, three 8 m plots were set up and monthly collections made of all seedlings appearing in the plots. Identification and counting of seedlings was undertaken in the laboratory by comparison with known samples under the stereoscopic microscope.

Diaspore numbers in the soil were monitored monthly by collecting the upper 2 cm of soil from four randomly set 50 × 50 cm quadrats. In the laboratory the soil was washed with 1 % sodium hypochlorite solution and after sifting through 35 mesh, the diaspores were separated, identified and counted under the stereoscopic microscope.

To measure diaspore production, we selected five healthy looking specimens in flower of each species. Shortly before diaspore release each plant was enclosed in a fine mesh material. After dispersal was completed, each whole plant including underground biomass was removed to the laboratory, diaspores collected and counted, and the aerial and underground biomass was washed and dried to constant weight. Diaspore production was expressed as number of diaspores per gram of dry weight of plant and as number of diaspores per individual plant; these measures probably represent the near optimum annual reproductive output. Furthermore, collected diaspores were examined under the microscope to detect the presence of a caryopsis. Caryopses were tested for viability using the tetrazolium test (MOORE, 1973). Simple germination tests were undertaken using three replicates of 100 caryopsis-carrying diaspores in Petri dishes under room conditions for three weeks.

Given the intention to highlight trends in seed bank dynamics and field germination, and due to the high variance imposed by horizontal patterns of distribution, data on diaspore numbers in the soil and on the appearance of new seedlings are shown as total numbers detected in the sampling, rather than mean values.

Data are presented here for the period February 1980 to December 1981. Prior to May 1980, the study site was under extensive cattle grazing, but since that time cattle have been totally excluded from the area. Extensive savanna fires in 1980 and 1981 affected the study area. On 26 February 1980

a first fire swept across most of the study area. The rest was burnt by a second fire on 13 March 1980. In 1981, a single fire swept across the whole area by the end of March. Also, a weather anomaly during 1981 created a break in the usually continuous dry season, due to unexpected rains during February which had ceased by the beginning of March.

## RESULTS

### 1. PHENOLOGY

Figures 1 and 2 present the results of the phenological tracking of the six species under study throughout 1980 and 1981. These curves do not represent rates of tiller formation or leaf growth but rather they show the proportion of the population actively producing new tillers, new leaves or reproducing. The latter includes floral development, fruit development and dispersal of diaspores.

Four different trends can be distinguished. In *Elyonurus adustus*, *Sporobolus cubensis* and *Leptocoryphium lanatum*, new tiller formation was restricted to the rainy season. *S. cubensis* peaked in tiller formation activity towards the end of the wet season, although this pattern was less marked in 1981. *L. lanatum* showed an inverse trend, peaking early in the wet season. *E. adustus* maintained a high level of tiller formation activity from May to December 1980 and again during the first part of the 1981 rainy season, but this activity declined progressively during the last months of the year. Production of new leaves for the three species was also maximal during the wet period, with no major differences between species, and it continued at a low level during the dry season.

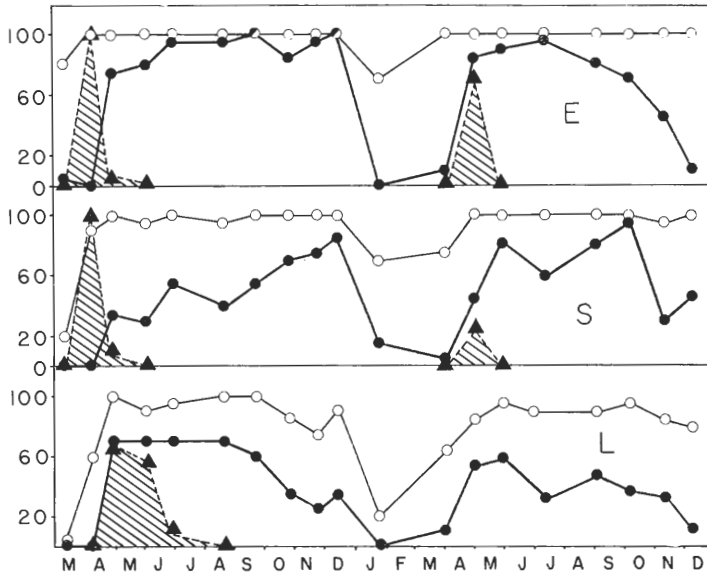


FIG. 1. — Phenological curves for *Elyonurus adustus* (E); *Sporobolus cubensis* (S) and *Leptocoryphium lanatum* (L). The abscissa represents months from March 1980 to December 1981. The ordinate is the percent of individuals in each of the three phenophases: a) producing new leaves ○—○; b) producing new tillers ●—● and c) reproducing (▲—▲).

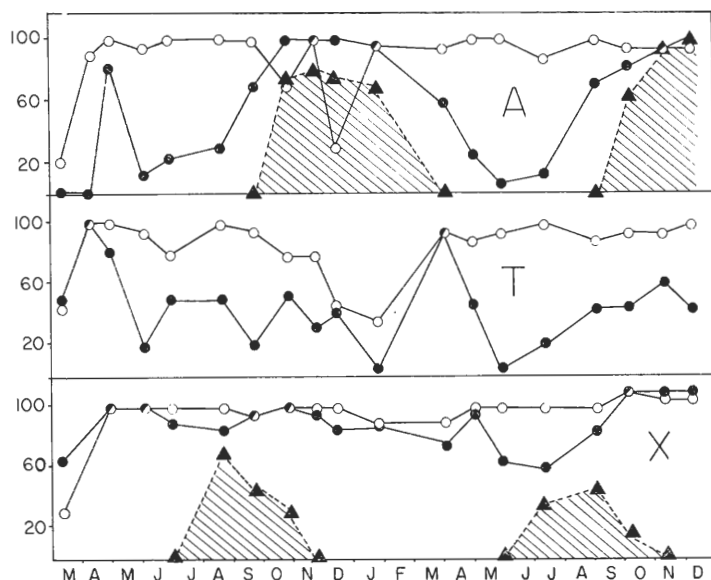


FIG. 2. — Phenological curves for *Andropogon semiberbis* (A); *Trachypogon plumosus* (T) and *Axonopus canescens* (X). For details see legend of figure 1.

These three species were also related in their reproductive phenology, flowering precociously by the end of the dry season and the beginning of the wet season. *E. cdustus* and *S. cubensis* bloomed a few days after the fire in both years, dispersal being very rapid after caryopsis formation. *L. lanatum* bloomed about a month later in 1980, and its reproductive period was about a month longer because of slower dispersal. None of the marked plants of this species flowered in 1981. Observations in the surrounding areas revealed very few flowering individuals, corroborating the lack of blooming activity during that year.

A second trend in vegetative growth is shown by *Axonopus canescens*. The majority of the population was constantly producing new tillers and new leaves. This trend of constant production of new vegetative structures was confirmed by our observations on the total population and by preliminary unpublished data on tiller formation and mortality rates. Flowering and fruit formation took place during July-August and diaspore dispersal was prolonged until November.

The timing of tiller formation in *T. plumosus* differed radically from the above species, peaking by the end of the dry season and the beginning of the rains, and decreasing afterwards. Again we found maximum leaf production activity during the wet period, with low levels of production during the dry season. None of the twenty plants in our sample flowered during 1980 or 1981. From observations on the total population we estimated that a third of the population flowered in 1980 and in 1981. Flowering peaked in September and dispersal took place before the end of October.

*Andropogon semiberbis* produced new tillers from the end of the wet season (October) to mid-dry season (February). Shoot elongation took place during September and October and the peak of anthesis was in November. Dispersal was slow and

continued during most of the dry season. Most of the population was producing new leaves throughout the year, except during the last months of 1980 when tiller and flower production were peaking.

## 2. REPRODUCTION

Diaspores differ greatly between species. Those from *E. adustus*, *A. semiberbis* and *T. plumosus* are structurally complex, heavy and bulky, whereas those from *S. cubensis*, *L. lanatum* and *A. canescens* are much smaller, simpler and lighter. There seems to be no relation between diaspore weight and number of diaspores produced per year (table I). Although diaspore production differed between the two years, particularly in the precocious species, there were important differences between species (table I). An analysis of variance showed these differences to be significant ( $p < .01$ ) and a *t*-test pair comparison showed that in both years *A. canescens* and *A. semiberbis*, produced a significantly higher number of diaspores per plant's dry weight and per individual plant than the other species. *T. plumosus* produced as few diaspores as the precocious species.

TABLE I. — Data on reproductive output for the six studied species.

SPP.	1*	2*	3*	4*	5*	6*	7*	8*	9*
<i>E. adustus</i>	146	669	4.6	12.3	65	96	80	2.6	2.2
<i>S. cubensis</i>	681	549	7.4	20.6	100	89	88	0.5	0.7
<i>L. lanatum</i>	593	—	16.0	—	74	72	69	0.6	0.8
<i>A. canescens</i>	4051	2958	125.7	102.0	17	85	2	0.2	2.3
<i>T. plumosus</i>	759	528	4.4	2.4	17	63	0	1.6	0.5
<i>A. semiberbis</i>	9509	11897	133.3	148.0	26	40	1	1.4	19.7

- 1\* = Diaspores per individual plant 1981.  
 2\* = Diaspores per individual plant 1982.  
 3\* = Diaspores per gram dry weight 1981.  
 4\* = Diaspores per gram dry weight 1982.  
 5\* = Percent diaspores with caryopsis after dispersal.  
 6\* = Percent viable caryopsis.  
 7\* = Percent germinated caryopsis after dispersal.  
 8\* = Diaspore dry weight (mg).  
 9\* = Percent of total dry weight in diaspores (mean).

The proportion of diaspores carrying a caryopsis was much higher in precocious species than in the others studied. The proportion of diaspores having a non-fertilized perfect floret (taken as a measure of fertilization failure) was 30 and 53 % in *A. semiberbis* and *T. plumosus* respectively. This counts probably indicate that the low proportion of caryopsis-carrying diaspores in these species partially results from heavy predator pressure. Actually, many spikelets lacking a caryopsis were found to carry an insect larva inside, but neither the extent nor the nature of the predation was assessed.

All species except *A. semiberbis* displayed a high caryopsis viability (table I). Seeds from precocious species were ready to germinate immediately after dispersal, whereas seeds from the other three species exhibited dormancy (table I). *A. semiberbis*

had the highest annual investment in diaspores, almost twenty percent, *A. canescens* and *E. adustus* showed intermediate values (near two percent), while the others had values lower than one percent (table I). Using the data shown in table I, we estimated the annual mean contribution of new embryos per individual for each of the six species. Although these estimates are based on only one's year data (1980) and we did observe important between-year fluctuations, they could be considered as a first approximation. *T. plumosus*, the only one with extensive vegetative multiplication, showed the lowest annual progeny per mean individual with only 3 embryos per individual per year, whereas *A. semiberbis* showed the highest number with about 1,000 embryos per individual per year. The values for the other four species are intermediate and similar to each other (200 to 300 embryos per individual per year). The original data represent maximum reproductive output in the field, therefore these are overestimates of annual individual contribution to the population.

The peak of germination occurred during May and June for all six species (fig. 3 and 4). In the three precocious species (*S. cubensis*, *L. lanatum* and *E. adustus*), there was a peak in number of diaspores in the soil immediately after flowering, at the beginning of the rainy season. Germination seems to deplete this bank of diaspores since diaspores of these species were not found after September. It is after this September that dispersal of the other three species (*A. canescens*, *T. plumosus* and *A. semiberbis*) took place. An increase in diaspore numbers in the soil for each of these species was recorded towards the end of the rainy season, followed by a slow decrease during the dry period and a sudden depletion due to massive germination by the

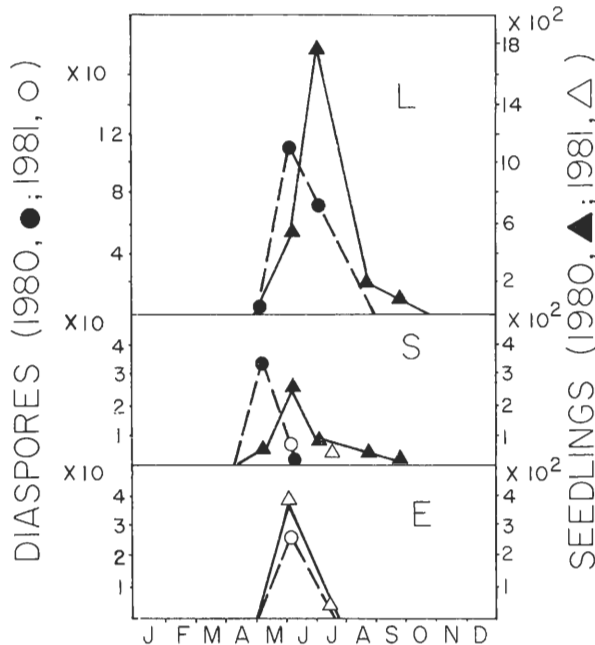


FIG. 3. — Diaspores found in the soil and seedlings harvested in the field. Numbers of diaspores are the sum of four 50 × 50 cm quadrats and numbers of seedlings are the sum of the harvests from three 8-square meter permanent plots.

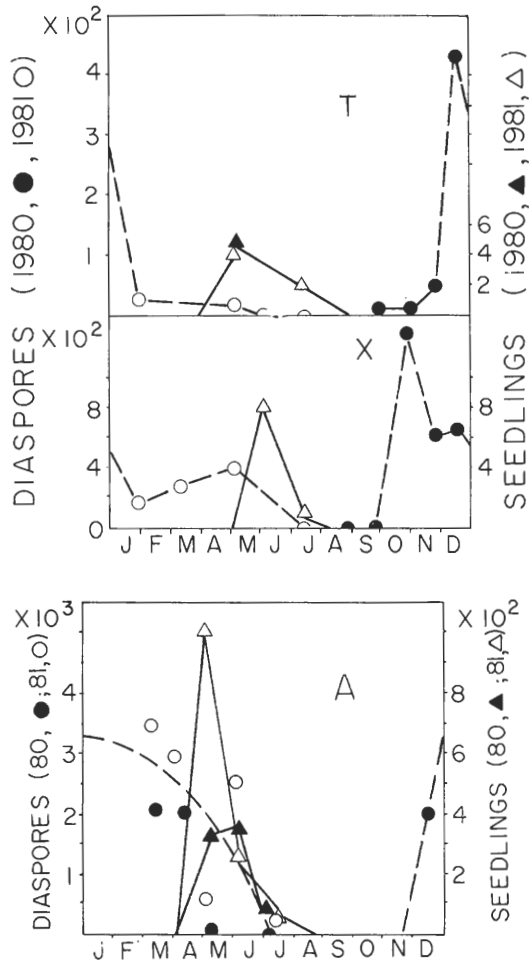


FIG. 4. — Diaspores found in the soil and seedlings harvested in the field. Numbers of diaspores and seedlings as in figure 3.

start of the following wet season. This evidence suggests that there is no permanent diaspore bank in the soil, but rather that it is annually refilled by each yearly flowering of the populations concerned.

Important differences in reproductive output occur between years. For instance, *L. lanatum* bloomed massively during early 1980 but failed to flower in 1981 and flowered again massively during 1982. Other species not considered in this study, like *Paspalum pectinatum* and *Andropogon selleanus* whose flowering peak coincides with that of *L. lanatum* were observed to show an inverse trend, blooming scarcely at all in 1980 but substantially in 1981. As shown in figures 3 and 4, seedling recruitment also changed from 1980 to 1981. Seedlings of *S. cubensis* were much more abundant in 1980 than in 1981; *E. adustus* seedlings, on the other hand, were not found in 1980



but were abundant in 1981. Also noticeable were the differences in number of seedlings on the ground for the different species: *A. canescens* and *T. plumosus* were scarcely found, whereas *L. lanatum* and *A. semiberbis* were abundant.

## DISCUSSION AND CONCLUSIONS

These results show that the six studied species differ in their vegetative and reproductive phenologies and that those species which flower well after the beginning of the rainy season postpone germination until the starting of the next year rains. Since this delay increases the risk of mortality during the seed stage, it could be compensated by producing more seeds. Two of the three late flowering species did produce significantly more diaspores than the other species, whereas *T. plumosus* produced as few diaspores as the precocious species. This is probably related to the fact that *T. plumosus* grows extensively by vegetative multiplication.

Phenological spread of codominant grass species is common in other savanna communities (RAMIA, 1977, 1978; SARMIENTO, 1983 *b*; MENAUT & CESAR, 1983) but there is no data on their reproductive output and germination.

GRIME (1979) pointed out that coexisting plant species which grow in different seasons of the year differ widely in their physiologies. Although venezuelan savanna climate has a dry-wet seasonality (MONASTERIO, 1969) the rainy season could be considered rather as three different periods (SARMIENTO, 1983 *b*). Phenological differentiation of grassland species seems to be related to temporal partitioning of nutrient resources but until very recently no direct evidences had been published (VERESOGLOU & FITTER, 1984). Flowering at different times during the growing season should imply different temporal patterns of energy flow in the plant which may be related to different temporal patterns in the use of limiting nutrient resources. On the other hand, RABINOWITZ *et al.* (1981) have suggested that flowering time spread in wind pollinated coexisting species may be avoiding interference between stigmatic surfaces, but no evidence is yet available to support this hypothesis.

Our results back the idea that phenological differences are related to differences in demographic programs (GRUBB, 1977). *A. semiberbis* seems to have the shortest life cycle with the highest annual reproductive output whereas *T. plumosus* is probably the most longevous of this group, with strong vegetative multiplication and low annual reproductive output. Although differences in regeneration dynamics have been proposed to explain coexistence (SARUKHAN, 1974; GRUBB, 1977; GRIME, 1979), the role of demographic differences allowing the coexistence of plant species competing for space is still unclear.

Maximizing the length of the first growing season may be of adaptive significance in communities with a marked seasonality (FRANKIE *et al.*, 1974). Thus, dormancy of *A. canescens*, *T. plumosus* and *A. semiberbis* seeds would have adaptive significance and could help to explain coexistence with the precocious species. Furthermore, the three species exhibiting seed dormancy probably differ in their dormancy mechanisms and diaspore dispersal syndromes since their seeds are dispersed under different environmental conditions. Thus, *A. canescens* and *T. plumosus* seeds are dispersed under the very humid conditions of the second half of the wet period and therefore stay in a very wet soil for several months. In contrast, *A. semiberbis* dispersal occurs during the first weeks of the dry season.

It seems that grass species coexisting in seasonal neotropical savannas are actively

reproducing by seeds and that they differ not only in growth and phenological patterns but also in their sexual reproductive dynamics and probably in their demographic patterns.

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