Patterns of specific and phenological diversity in the grass community of the Venezuelan tropical savannas

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ABSTRACT. The coexistence of several species of perennial grasses seems to be a definite trait of most tropical savannas. To analyse this feature, trying to relate this co-occurrence to environmental and ecosystem characteristics, two samplings were designed, one involving the whole savanna area in Venezuela, the other restricted to a climatically more homogeneous area within the Venezuelan western llanos. Through the use of indexes of specific and phenological diversity, it is shown that all Venezuelan seasonal savannas have a combination of perennial grasses showing relatively medium evenness values. This specific diversity was partly explained by the phenological diversification of the grass community that leads to a temporal division of the niche. An analysis of phenological diversity and the patterns of occurrence of each phenological group in terms of climatic and soil factors, leads to the conclusion that each group represents a definite species guild more or less favoured by distinctive habitat conditions. Moreover, the unpredictability of some environmental constraints, like the extension of the rainy season when soil water is available to grasses, as well as the precise annual timing of fires, seems to have contributed to the maintenance of both high specific and phenological diversities in the grass community of this type of tropical ecosystem.

Introduction

Biological richness and specific diversity appear as two of the most conspicuous features of lowland tropical terrestrial ecosystems, either at the level of the whole systems or just taking into account partial components of the biocenosis (Fisher, 1960; Pianka, 1966; Lowe-McConnell, 1969; MacArthur, 1972). This fact has been extensively evidenced in humid forests of all tropical regions (Ashton, 1964; Fedorov, 1966; Hallé *et al.*, 1967; Letouzey, 1969; Richards, 1969; Murça Pires, 1978) whereas available data on other tropical communities are much more scarce. In tropical American savannas in particular, floristic inventories suggest relatively high richness and diversity (Eiten, 1963; Van Donselaar, 1965; Sarmiento

& Monasterio, 1969; Silva & Sarmiento, 1967a, b), but unfortunately these aspects have not been further analysed.

Patterns of species abundance and diversity in multi-species communities have been the core of fertile disputes and opposing views in recent ecological literature and they contribute in many ways to significant advances in ecological theory. We may refer, among many others, to the critical books and articles by MacArthur (1972), Whittaker (1972), Schoener (1974), May (1975, 1976), Pianka (1976), Connell (1978), Blondel (1979) and Grassie *et al.* (1979). The particular situation in species-rich plant communities has been considered by Whittaker (1977), Grubb (1977) and Grubb, Kelly & Mitchley (1982). May (1979), summing up the conclusions of an important symposium on population dyna-

mics, makes the following statements that aptly describe the actual situation in this field. He says that 'a good understanding of the observed dynamics of single populations is currently emerging.' In contrast, 'the survey of multispecies systems could only list some empirical patterns that are as yet largely unexplained' and 'a list of questions about the structure and dynamics of these systems'. These conclusions suggest that more field data concerning as many different ecosystems as possible have to be available to allow valid generalizations and more robust models describing multispecies interaction.

Up to now, relevant field data supporting theoretical generalizations come largely from studies on the avifaunas, the herpetofaunas, and other vertebrate taxocenosis in various temperate and tropical ecosystems. Much less came from tropical forest trees or other plant components of terrestrial communities, while the analyses of factors related to grass diversity and relative abundance of grass species in grasslands in general and in tropical savannas in particular, are yet in their very beginnings (McNaughton, 1978; Bergh, 1979; Sarmiento, 1981; Silva & Ataroff, 1983).

Perennial grasses constitute the dominant species in savanna ecosystems besides being the most important group for possible improvement of the management of natural vegetation. The aim of this study is to compare a wide set of savanna communities with regard to coexistence and codominance of perennial grasses, in order to discover the possible roles of environmental and other factors in the divisions of the global niche among them. Through this, we hope to gain a closer acquaintance with this economically valuable component of the ecosystem.

We limited our scope to a well-defined type of ecosystem: the seasonal savanna, as it occurs in Venezuela. The ecological characterization of seasonal savannas was presented elsewhere (Sarmiento & Monasterio, 1975). In brief, this ecosystem differs from other related types, especially from hyperseasonal savannas, because it overpasses one single water stress during its annual cycle. A more or less severe drought period lasting from 3 to 6 months represents the crucial environmental stress for the seasonal savanna. In contraposition to hyperseasonal savannas,

the soil never becomes waterlogged and hence soil water excess could not represent a handicap to plant life. But even during the rainy season, in spite of a large water surplus, shallow-rooted species may suffer from short periods of drought due to high evapotranspiration and desiccation of the superficial soil layers (Sarmiento & Vera, 1977).

Species of perennial grasses occurring in Venezuelan seasonal savannas show strong similarities in gross morphology and architecture, including many features that can be related to the maintenance of a favourable water balance throughout the year. Most of them show the characteristic tussock growthform and they reach a vegetative height of about 1 m. Their root systems mainly exploit the upper soil horizons, rarely extending beyond 1 m depth (Sarmiento & Vera, 1979). There is some reason to suspect that water and mineral nutrients are the two most critical limiting factors for these species (Silva & Sarmiento, 1976b), and as all of them presumably rely on the same soil layers, the actual modalities of niche partition pose the question of how several rather similar species coexist competing for the same limiting resources.

In previous papers we postulated that a temporal partition of critical resources was the main mechanism operating to avoid competition in this system (Sarmiento, 1978, 1980, 1981; Sarmiento & Monasterio, in press). In fact, the various species of perennial grasses differ widely from each other in their annual phenodynamics, especially in what concerns their periods of maximum growth and sexual reproduction. At least in the best-known savanna communities of the western Venezuelan llanos, the codominant grasses bloom in sequence one after the other, from the last weeks of a dry season to the beginning of the next drought period. In this sense, they form a continuum of phenological groups only partially overlapping and mostly replacing each other, so all together their reproductive periods occupy the most favourable part of the annual cycle, since only the two driest months do not show the blooming of some perennial grass.

To start with, we posed the following questions: (1) How many species of perennial grasses coexist in tropical savanna communi-

ties occurring on different soils, under different climates and submitted to various management practices? (2) Is there any relation between codominance and temporal partition of the niche? (3) Along which environmental axis do perennial grasses partition the critical resources for their survivorship under the hard conditions of tropical savannas? (4) Is it possible to establish any clear relation between diversity, partition of resources and environmental factors?

To answer these questions we designed a quantitative sampling of a wide set of seasonal savannas in Venezuela. The research was planned at two different levels of vegetation and environmental heterogeneity. First, we compared the situation in savannas that occur within the same region, a restricted area of the western llanos, under similar climate, but that differ from each other in soil characteristics. Second, we extended the analysis to the whole range of environments and savanna communities occurring in Venezuela. By this double analysis we attempt to clarify the

relative role of environmental and other factors on species diversity and resource partition.

Methods

Field data

Forty-two stands of seasonal savanna were sampled to embrace all Venezuelan regions where this ecosystem has a local importance in the vegetation cover (Fig. 1 and Table 1). Each stand was selected on the basis of three criteria. First, to be a seasonal savanna; second, to have an extension of at least a pair of hectares without noticeable changes in topography, soil and composition; third, to be in an apparently stable condition, that is, without major signs of human impact other than extensive cattle grazing and fire (this last is considered as normal ecological stress in the savanna ecosystem).
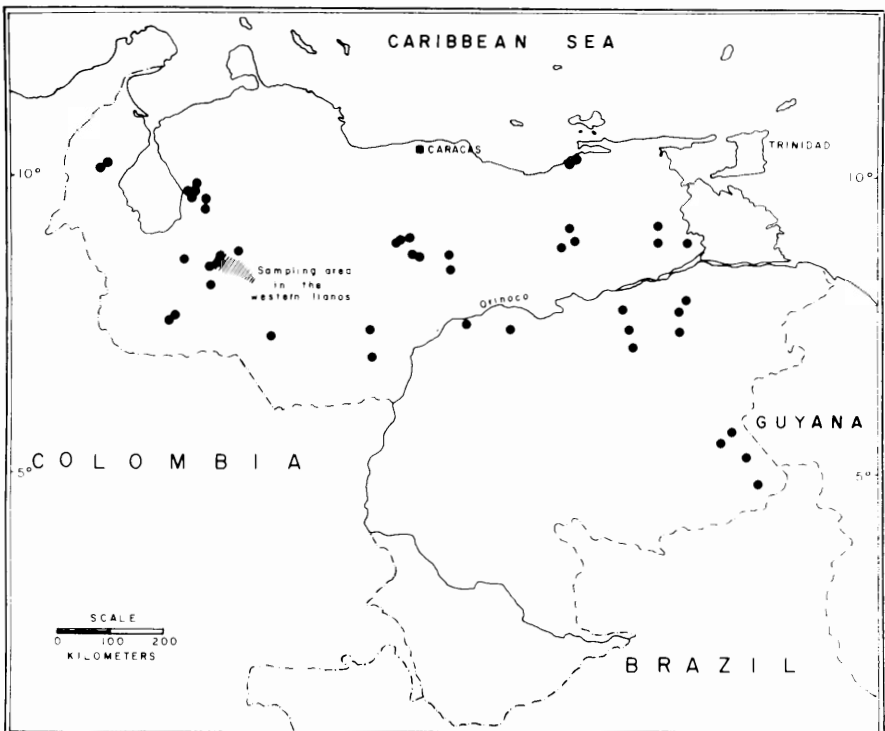
Within each stand 100 square quadrats,

FIG. 1. Location of the savanna plots in Venezuela. Notice also the location of the small, intensively sampled area in the western llanos.

TABLE 1. Some environmental features together with characteristics of the perennial grass community in the savanna plots of the Venezuelan sample

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Annual rainfall (cm)	110	110	140	260	100	110	160	110	140	110	120	130	120	80	80	100	100	100	120	120	120
April rainfall (cm)	75	75	100	125	25	50	75	75	75	75	75	75	75	25	25	25	25	25	50	50	50
November rainfall (cm)	50	50	50	75	75	75	75	75	75	75	100	150	100	100	100	50	50	50	50	50	50
Soil depth*	5	d	d	d	d	d	s	s	d	s	d	d	d	s	s	d	d	s/d	d	d	d
Number of perennial grass species S	5	9	7	7	5	8	9	7	6	7	7	6	5	12	3	8	10	11	9	5	7
Relative frequency of precocious grasses	19	3.5	10.8	24	9	28.4	5.4	0.4	3	0.5	0	0	0	6.3	0	1.5	21	16	4	0	9
Relative frequency of early-blooming grasses	20	25	41	31.4	41	27.4	22	31	42.5	37	57	47.5	49	53.3	16	38	35.3	37	52.5	56	57
Relative frequency of intermediate-blooming grasses	53	64	44	45	46	41.4	59	64	51	47	41	51	50	36.3	81	59.5	36.3	41	36	21	35
Relative frequency of late-blooming grasses	8	7	5	0.8	3	2	14	3	3	15	2	1	1	3	3	2	05	7	7	23	0.4
Relative specific diversity D'	0.58	0.18	0.27	0.36	0.46	0.46	0.33	0.41	0.27	0.33	0.53	0.38	0.43	0.25	0.22	0.18	0.32	0.49	0.40	0.42	0.47
Relative phenological diversity D_f	0.58	0.36	0.55	0.60	0.52	0.68	0.46	0.32	0.42	0.54	0.34	0.35	0.35	0.46	0.16	0.34	0.76	0.66	0.48	0.48	0.40

	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Annual rainfall (cm)	120	120	180	180	180	180	160	160	200	200	180	150	180	120	120	100	130	130	120	120	120
April rainfall (cm)	50	50	150	150	150	150	150	150	150	150	150	150	150	125	125	125	75	75	125	125	125
November rainfall (cm)	50	50	125	125	125	125	100	100	150	150	125	100	100	150	150	150	75	75	150	150	150
Soil depth*	s	s/d	s	d	s	d	d	d	d	d	d	s	d	s/d	s	d	s/d	d	d	s/d	s
Number of perennial grass species S	4	6	9	9	8	8	8	9	12	11	7	7	8	6	4	4	9	7	5	4	3
Relative frequency of precocious grasses	29	41	0.8	0.3	0	0.2	42	28	53.6	64	0	7	71	2	3	4	0.3	11	1.5	0	0
Relative frequency of early-blooming grasses	17	14	13	24	5	5	25	49	33.6	12	64	53	28	25	10	19	58	66	42	46	38
Relative frequency of intermediate-blooming grasses	38	42	77	56	36	41	17	8	6.3	7	36	34.8	0	55	87	78	26	23	52	53	59
Relative frequency of late-blooming grasses	16	4	10.5	19	58	53	16	15	7	17.2	0	4	1	17	0	0	17	0	5	2	3
Relative specific diversity D'	0.84	0.37	0.52	0.55	0.53	0.72	0.77	0.57	0.35	0.54	0.61	0.39	0.40	0.35	0.08	0.17	0.55	0.64	0.29	0.34	0.51
Relative phenological diversity D_f	0.84	0.58	0.20	0.49	0.38	0.41	0.80	0.63	0.48	0.39	0.29	0.48	0.24	0.51	0.10	0.18	0.44	0.33	0.41	0.34	0.34

* S = shallow;   d = deep;   s/d = variable within the plot.

each of 1 m side, were taken. They were regularly spaced along two parallel transects 10 m apart from one another. On each line quadrats were taken at an average distance of 5 m, but the precise location of each sampling unit was the product of a blind selection to avoid any subjectivity in the sampling procedure. In this way, the quadrats were distributed more or less regularly over an area of about 250×10 m. The purpose of this sampling design was to include most internal floristic variability within each stand, in order to obtain a representative sample from a large area of savanna.

In each quadrat, delimited by a metal frame at the soil surface, all rooted perennial grasses were listed and their phenology was noted, as well as several features about the relief, soil, vegetation structure, and actual land use. Monthly rainfall data concerning each site were obtained from the Venezuelan Climatological Atlas (República de Venezuela, 1957).

Apart from this sampling designed to cover the whole range of environmental variability under which seasonal savannas occur, we utilized a second set of field data on the various types of savanna communities occurring within a rather restricted area (Fig. 1) under relatively uniform climate but on different topography and soil type. These data were obtained in a previous research on the composition of savanna communities along topographic gradients in the western Venezuelan llanos (Silva & Sarmiento, 1976b). They consist of ten random samples from each of the five seasonal savanna types occurring in this area, each community defined on the basis of an homogeneous soil unit (Soil Series). Each sample was a 100 m^2 quadrat where all plant species were listed and plant cover determined by means of 100 random points. In this manner, the total list of perennial grasses in a 100 m^2 sample was obtained, together with the cover (or frequency) of each species by the point-quadrat method.

Obviously, the two sets of data are not comparable with each other since the sampling procedure and the attributes sampled were not the same in the two cases. For this reason, we carried an independent analysis with each set, but the conclusions will be later discussed together since they refer to the same underlying ecological features characterizing this kind of ecosystem.

Plant identification was almost always possible in the field. Rarely, some vegetative tillers had to be carried to the laboratory for comparison with herbarium material and definite identification. Plant names follow the nomenclature used in the Venezuelan National Herbarium.

In previous papers (Monasterio & Sarmiento, 1976; Sarmiento & Monasterio, 1982) the phenologies of various savanna grasses were considered. These data, together with numerous field observations assembled during many years over many types of Venezuelan savannas, were utilized to complete the phenological picture in order to establish the various types of phenodynamics within the perennial grass community.

Methods of analysis

Total number of perennial grasses (S) as well as the frequency of each species (Fr, equivalent to cover in the case of the point-quadrat method) were computed for each stand. As a measure of evenness we employed an index derived from Simpson's coefficient of diversity:

$$D = 1/\epsilon_i p_i^2$$

In our case $p_i = \text{Fr}_i$. MacArthur (1972) points out how this index may be as convenient as any other of those currently utilized in ecology, besides having the advantage of easiness of computation and clearness in interpretation. To compare samples with unequal richness, setting apart the influence of richness from that of evenness in the diversity index, we recur to a coefficient of relative diversity D' equal to:

$$D' = D - D_{min}/S - D_{min}$$

This measure of evenness that does not depend on S is called V by Pielou (1975). It represents the relation between actual and maximum possible diversity with a given number of species. The maximum possible value of D is S, the minimum is $100/(100 - S + 1) + (S - 1)$. D' then varies between 0 and 1.

Once all the species of perennial grasses found in our samples were assembled into

four phenological groups according to their annual phenodynamics, the relative frequency of each group in every stand was computed, as well as two indexes related to phenological diversity: D_f and D'_f, in a similar way as the two previous indexes of specific diversity D and D' were obtained. That is:

$$D_f = 1/\epsilon_i p_i^2$$

where p_i is the relative frequency of each phenological group in a given plot. This co-efficient may vary from 1, when just one phenological group does occur, to 4 in the case of a perfectly even representation of the four groups. We then transformed this measure into an index of relative phenological diversity:

$$D'_f = \frac{D_f - D_{f\min}}{D_{f\max} - D_{f\min}} = \frac{D_f - 1}{3}$$

Results

Species diversity

A total number of forty-five species of perennial grasses was found in the forty-two savanna stands sampled in the whole country. The number of grass species per stand varied from three to twelve, with a mean of 7.2 and a standard deviation (σ) of 2.3 (Fig. 2A). In the fifty samples of the western llanos, the number of perennial grass species per stand ranged from four to thirteen, with a mean of 9.0 and a σ of 2.0 (Fig. 2B). All together, in these fifty samples, a total of twenty-seven perennial grasses was recorded.

According to these figures, we may see that the coexistence of several perennial grasses in each savanna stand appears as a general feature of this ecosystem. More than one grass species is always present; most commonly from five to eleven perennial grasses coexist in any given stand.

Considering the specific diversity in the forty-two Venezuelan samples (Fig. 3A) we may appreciate that the average relative diversity D' was 0.42 with a σ of 0.16. As these two figures indicate and the graph shows, medium values of about half the maximum possible diversity or a few less, are most frequent, suggesting that there is neither
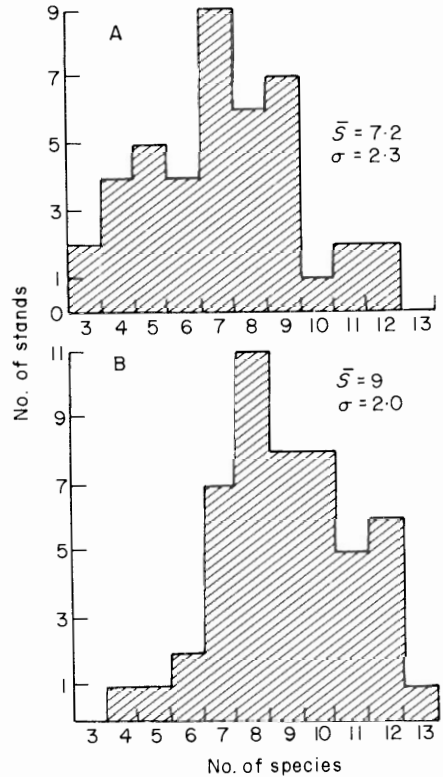

FIG. 2. Number of perennial grass species per savanna stand: (A) in the Venezuelan sample; (B) in the western llanos sample.

an even mixture of the several grasses nor a clear dominance of one or two species in each stand. In the fifty samples of the western llanos, a mean relative diversity of 0.45 was obtained with a σ of 0.16 (Fig. 3B). These savannas, then, also show medium values for evenness.

Phenological patterns

The most remarkable phenological feature arising from our field observations is that the several grasses do have their times of most active growth and flowering scattered through the vegetation annual cycle. When all the grass species are taken into account, there always is at least one grass population in bloom during the whole period extending from a few days after burning to the middle or even to the last part of the following dry season. We must remember that in Venezuela seasonal savannas occur under a typical wet and dry
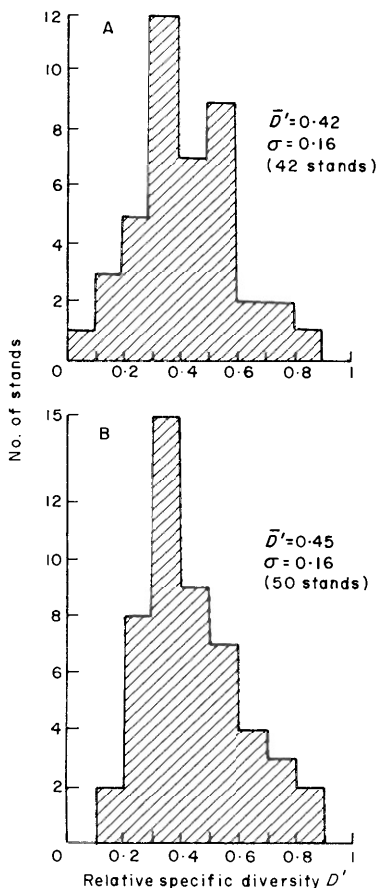
FIG. 3. Relative specific diversity D': (A) in the Venezuelan sample; (B) in the western llanos stands.

tropical climate, with two sharply defined seasons: a rainy season from April or May to October or November, and a dry season from November or December to March or April. April and November being wet or dry months, according to certain regional climatic trends (Monasterio, 1970).

A further fact to remember is that seasonal savannas are regularly burned towards the end of the dry season (February to April), that is, just a few weeks before the first rains. Thus burning promotes an early growth in many species that will proceed further with the onset of rains. In burned savannas, the annual cycle of shoot-growth and flowering may start either in February or in March, or even in April, according to the precise date of burning during that particular year. Growth and development will continue at various specific

rates till December, or more exceptionally to January, when drought hinders any further plant activity within the grass community. If a savanna remains unburned during a given year, its growth-cycle will start after the onset of rains and last to December or January, but there are not noticeable signs of activity before the beginning of the rainy season. All along this 8–10 month growth-period one or another grass will have its peak of vegetation and reproductive activity. Table 2 summarizes the data on blooming periods for the perennial grasses in Venezuelan seasonal savannas, when regularly burned at the end of the dry season.

To simplify the phenological picture of the perennial grass community, we grouped all these species into four different phenological groups established according to the times of occurrence of their flowering peaks. A first group of 'precocious grasses' includes the species that may start blooming from before the onset of rains (February) to others that begin to flower about 2 months after the arrival of the rainy season (May). A second phenological group includes the grasses that bloom after the first group but during the first half of the rainy season, that is, from May to July. These are the 'early flowering species'. A third group of 'intermediate-flowering grasses' blooms during the second half of the rainy season, i.e. from August to October. Finally, the 'late-flowering species' have their reproductive peaks towards the end of the rainy season or during the first part of the dry season, that is, from October to January.

Naturally, this grouping oversimplifies the phenological picture of the grass community and is based on conventional temporal limits. Certain species show a more sophisticated behaviour, either with a long blooming period or even with two flowering peaks. But in these particular cases the species was included in a phenological group according to its first date of blooming, because the whole developmental pattern of any species is sharply influenced by the onset of its reproductive phenophases. Moreover, the limits between groups were taken in such a way that each group could represent one kind of coherent ecological behaviour, avoiding a too detailed differentiation that would lead to a high

TABLE 2. Classification of perennial grasses of the Venezuelan seasonal savannas into four phenological groups according to period of flowering and maximum growth

Precocious (February—May)	Early (May—July)	Intermediate (August—October)	Late (October—January)
Andropogon selloanus (Hack.) Hack	Aristida pittieri Henr.	Aristida recurvata H.B.K.	Andropogon hirtiflorus (Nees) Kunth.
Elyonurus adustus (Trin.) Ekman	Axonopus affinis Chase.	Aristida riparia Trin.	Andropogon semiberbis (Nees) Kunth.
Imperata contracta (H.B.K.) Hitchc.	Axonopus anceps (Mez) Hitchc.	Aristida tincta Trin. & Pilger.	Axonopus kaietukensis Swallen.
Leptocoryphium lanatum (H.B.K.) Nees.	Axonopus canescens (Nees & Trin.) Pilger.	Paspalum contractum Pilger.	Axonopus pruinosus Swallen.
Paspalum carinatum Humb. & Bonpl.	Axonopus chrysoblepharis (Lag.) Chase.	Paspalum hyalinum Nees.	Echinolaena inflexa (Poir.) Chase.
Paspalum pecthnatum Nees	Axonopus compressus (Swartz) Beauv.	Schizachyrium tenerum Nees.	Hyparrhenia rufa (Nees) Stapf.
Sporobolus cubensis Hitchc.	Axonopus pulcher (Nees) Kuhlm.	Trachypogon montufari (H.B.K.) Nees.	Melinis minutiflora Beauv.
	Axonopus purpusii (Mez) Chase.	Trachypogon plumosus (Humb. & Bonpl.) Nees.	Panicum polycomun Trin.
	Mesosetum chaseae Luces.	Trachypogon vestitus Anders.	
	Panicum olyroides H.B.K.		
	Panicum coryphaeum Trin.		
	Paspalum chaffanjonii Maury		
	Paspalum gardnerianum Nees		
	Paspalum multicaule Poir		
	Paspalum notatum Flugge		
	Paspalum plicatulum Michx		
	Paspalum stellatum Humb. & Bonpl.		
	Paspalum virgatum L.		
	Setaria geniculata (Lam.) Beauv.		
	Sorghastrum parviflorum (Desv) Hitchc. & Chase.		
	Sporobolus indicus (L.)R.Br.		
	Thrasya petrosa (Trin.) Chase.		

TABLE 3. Presence/absence of each phenological group of perennial grasses in the seasonal savanna stands of the Venezuelan and the western llanos samples

Phenological groups	Forty-two Venezuelan stands		Fifty western llanos stands	
	+	−	+	−
Precocious-blooming	33	9	50	0
Early blooming	42	0	50	0
Intermediate-blooming	41	1	47	3
Late-blooming	38	4	42	8
Four groups present	32		39	
Three groups present	9		11	
Two groups present	1		2	

number of groups difficult to correlate with ecological variables. In any case, the phenological analysis emerging from this grouping has to be considered just as a first rough approximation that could be later complemented by considering the phenodynamics of each species as a distinct entity.

Phenological diversity

After this first generalization about the wide range of phenological responses among the flora of perennial grasses, we have to consider now the situation in each stand in order to disclose if some communities have a predominance of one particular type of phenodynamics or, on the contrary, to see if the various phenological groups are more or less evenly represented in each stand.

Table 3 shows the results obtained in both samplings. As may be observed, in most stands the four phenological groups coexist, in about a quarter of the samples only three groups appear, while two groups occur in just one of the forty-two Venezuelan samples and in two of the fifty western llanos stands.

Of the four phenological groups, the early-blooming occurs in every stand, the intermediate-blooming is lacking in a few samples, while the precocious-blooming does not appear in nine Venezuelan samples and the late-blooming in four Venezuelan and eight western llanos stands.

Referring then, to the presence or absence of each of the four groups of grasses we established according to their reproductive peaks, the previous figures seem to indicate that a mixture of species having contrasting phenological behaviour coexist in most seasonal savannas.

To quantify phenological diversity, the index D_f' was calculated for each savanna plot. Fig. 4A shows the distribution of relative phenological diversity in the forty-two
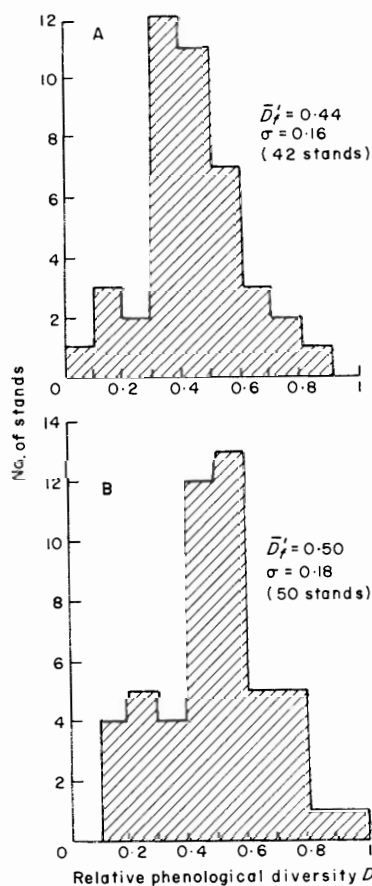

FIG. 4. Relative phenological diversity D_f' per savanna stand: (A) in the Venezuelan sample; (B) in the western llanos stands.

Venezuelan stands, while in Fig. 4B the same index for the fifty western llanos samples is shown. In the first case, a mean index of 0.42 was obtained with a σ of 0.16. In the savannas of the western llanos, the mean index was 0.50 with a σ of 0.18.

These figures confirm the previous conclusions on phenological diversity, pointing out that the most common situation in these savannas seems to be a rather even combination of grasses having different phenological patterns, whereas very seldom a net dominance of any given phenological group does occur. That is, the phenological picture is comparable to that emerging from the analysis of specific diversity, since in both cases medium degrees of evenness are the rule. However, no significant correlation between the two diversities: specific and phenological, could be demonstrated ($r = 0.43$ for the Venezuelan savannas and $r = 0.11$ for the western llanos stands).

Diversity and environment

After realizing the significant specific and phenological diversities that were apparent in the perennial grass community of seasonal savannas, the next step is the search for possible relationships between plant diversity and various external driving forces acting upon this ecosystem. To do that, we selected the most relevant climatic and soil factors to test their correlation with the two diversity indexes D' and D'_f.

Annual rainfall and soil depth appear as the two environmental factors more sharply differing among the savannas in the Venezuelan sample. Annual rainfall within the Venezuelan savanna area ranges from 800 to more than 2500 mm (Table 1). Although precipitation always shows the same distinctive seasonal pattern, April and November, the two transitional months between the dry and the moist season vary regionally from rainy to dry. To simplify the situation, we took each of these months as rainy when precipitation was 100 mm or more, while they were considered as dry when monthly rainfall was less than 75 mm. Thus, mean annual precipitation together with rainfall in the two transitional months, were taken as three climatic variables that might account for differences in diversity between

savanna communities. Furthermore, after the first results discussed below were obtained, we decided to proceed with the analysis setting apart two categories of sites: those relatively rainy, where annual precipitation was 1600 or more mm, and those relatively dry, where rainfall was below 1100 mm. This separation of the relatively moister from the drier sites was then introduced into the diversity analysis.

Soils are the other component of the savanna ecosystem showing wide regional variation, in spite of the fact that all these soils are quite similar in many physical and chemical features (Sarmiento, 1978). Thus, they all have fairly leached profiles, with medium to coarse texture, rather low organic matter content (about 1% in the A_1 horizon), high acidity (pH from 4.0 to 5.5), very low cation-exchange capacity (mostly below 4 meq/100 g of soil), and also a feeble base saturation (below 20%). All these features together make savanna soils extremely poor in nutrients. But besides these common characteristics, soil depth appears as the principal single factor differing most among our sample plots. In fact, some soils show a deep profile developed in old alluvial materials. But other savannas occur on shallow soils where root penetration is hindered by one of two causes. First, on hard standstones, the soil seldom attains more than 10 or 15 cm in depth. Second, in many areas corresponding to early Quaternary relictual surfaces ('mesas'), hard plinthic horizons were formerly developed and later disaggregated by erosion, giving rise to a sort of rock pavement where root penetration is hardly possible. But whatever could be the cause, all shallow soils are relatively dry because the small soil volume exploited by roots, particularly by the fine roots of grasses. These two sharply contrasted soil-depth categories were taken to assess their impact on grass diversity.

Considering now the situation in the western llanos, the major environmental factors differing most among our savanna samples are related to the water regime in the soil. Let us remember that this area represents a relatively moist section of the whole rainfall gradient under which seasonal savannas do occur. Annual rainfall always exceeds 1400 mm, with the rains

TABLE 4. Specific and phenological diversity within the perennial grass community of seasonal savannas in Venezuela under various environmental conditions. Asterisks indicate significance at the 0.05 and 0.01 levels.

	All sites in Venezuela	Dry sites Rainfall ≤ 11 cm	Rainy sites Rainf. ≥ 16 cm	April		November		Soils	
				Dry	Rainy	Dry	Rainy	Shallow	Deep
No. of stands	42	12	23	23	19	20	22	12	25
Mean number of perennial grass species S	7.2	7.4	8.8*	7.2	7.2	7.3	7.1	6.6*	7.5"
Index of relative specific diversity D'	0.42	0.34**	0.52**	0.40	0.44	0.42	0.42	0.42	0.42
Index of relative phonological diversity D'_f	0.44	0.46	0.45	0.46	0.41	0.52**	0.37**	0.41	0.45
Relative frequency: precocious species	12.4	9.1	24.1**	9.1**	16.4**	11.8	12.9	6.0	15.6**
Relative frequency: early species	34.8	31.7	26.0*	39.0*	29.7	37.5	32.3	26.3*	38.7*
Relative frequency: intermediate species	43.7	54.0*	32.4*	45.4	41.7	43.6	43.8	56.3*	37.9*
Relative frequency: late species	9.1	4.8*	17.6*	6.5	12.3*	7.1	10.9*	11.4*	7.8

already starting in April and extending to November. The climatic factors setting apart the samples in the Venezuelan sample cannot then be used in this more restricted and climatically homogeneous area. Furthermore, all these savannas occur on deep soils, since neither sandstones nor iron hardpans occur in this area. The savanna stands in the western llanos represent a series of communities roughly corresponding to a topographic sequence of increasing soil humidity starting from relatively high sites with coarse-textured and excessively drained soils (Q_{iv}) to low sites with medium-textured and imperfectly drained profiles (Garza). The main emphasis in our analysis of environmental factors responsible for grass diversity is given then to this major humidity gradient.

The results of the analysis of diversity under different environmental conditions appear summarized in Table 4 for the Venezuelan stands, and in Table 6 for the savannas in the western llanos. The vegetation variables included are the mean number of perennial grass species (S), relative specific diversity (D'), relative phenological diversity (D'_f), as well as the relative frequency (Fr) of each of the four phenological groups. The more interesting points emerging from the study of the Venezuelan sample are:

(1) Neither the number of perennial grasses nor specific or phenological diversity were correlated with total annual rainfall.

(2) The mean number of grass species per sample is lower in the dry sites than in the rainy ones (7.2 v 8.8). This number is also significantly greater in deep than in shallow soils (7.5 v 6.6).

(3) No significant relation appears between Fr of precocious, early and intermediate-blooming species and total annual rainfall. This climatic parameter only appears significantly correlated with the Fr of late-blooming grasses.

(4) Considering separately the samples in the more rainy and in the drier areas, that is, disregarding the intermediate sites with annual rainfall between 1100 and 1600 mm, mean specific diversity is greater in the rainy than in the dry plots (0.52 v 0.34) being this difference significant at the 0.01 level.

(5) Of the four environmental factors tested, mean phenological diversity only varies with November rainfall by increasing in sites where this month is comparatively dry and decreasing where it is comparatively moist.

(6) The Fr of precocious-blooming grasses increases most in the rainy group of savannas, then in those with a rainy April, and then on deep soils. The opposite trend is also evident, since this phenological group decreases its Fr on shallow soils, the dry group of savannas and those with dry Aprils. On the contrary, November rains do not have any noticeable influence on the relative abundance of precocious species.

(7) The Fr of early blooming grasses increases most on deep soils and in sites with dry Aprils and Novembers. In the opposite circumstances, as well as in the relatively rainy sites, its Fr decreases.

(8) The Fr of the intermediate-blooming group of grasses noticeably increases above the mean in the dry sites and on the shallow soils decreasing concomitantly in the rainy sites and on deep soils.

(9) The Fr of the late-blooming species sharply increases in the rainy plots and in sites where April and November are relatively moist months. They also become more abundant on shallow soils while it decreases with the opposite conditions: less rainy sites, dry Aprils and Novembers, and deep soils.

Table 5 summarizes the behaviour of each phenological group in relation to rain and soil conditions. It is shown how the precocious group seems to prefer relative moister climates, particularly when the rains already start in April, but within these conditions it increases its relative frequency on shallow soils with low water storage capacity. The early blooming group also increases on these soils but becomes restricted mostly to relatively dry climatic conditions where the rainy season is shortest. The other two groups colonize preferentially deep soils, with a higher water storage capacity but separate according to climate: the late-blooming grasses being more frequent on moister areas while the intermediate-blooming species restrict more to drier areas.

Finally, analysing the association between the occurrence of the various phenological groups, it is shown that the Fr of precocious and early blooming species are inversely cor-

TABLE 5. Some relationships between climate, soils and frequency of phenological groups of perennial grasses in the Venezuelan seasonal savannas. Each group attains its maximum relative frequency under a different combination of environmental factors.

Soils	Climate		
		Relatively moist long rainy season	Relatively dry short rainy season
Shallow; low water storage		Rainy season from May to November; late	Rainy season starts in May; intermediate
Deep; high water storage		Rainy season from April to October; precocious	Rainy season from May to October; early

related, the same applies to early and intermediate-blooming grasses. That is, each phenological group seems to have its own optimum in the environmental mosaic.

Considering now the situation emerging from the analysis of the savannas in the western llanos (Table 6), the main points may be summarized as follows:

(1) The number of perennial grass species per sample increase slightly in the moister part of the humidity gradient.

(2) Relative specific diversity D' is highest in the driest savannas (Q_{iv}), then it falls sharply to increase again slowly towards the moister soils.

(3) Relative phenological diversity D'_f attains its maximum values in the middle of the moisture gradient (Barinas series).

(4) The relative frequency of precocious species steadily decreases with increasing soil moisture.

(5) Fr of early blooming grasses shows exactly the reverse trend, increasing towards the moister part of the gradient.

(6) Fr of intermediate grasses attains its maximum in the middle of the moisture gradient, while its minimum is attained in the driest types of savannas.

(7) Fr of late-blooming species is maximum in the middle of the gradient and decreases to its minimum in the moister communities.

TABLE 6. Specific and phenological diversities within the perennial grass community of seasonal savannas on various soil series in the Venezuelan western llanos

	All sites in the Western llanos	Soil series				
		Q_{iv}	Boconoito	Barinas	Camoruco	Garza
No. of stands	50	10	10	10	10	10
Mean number of perennial grass species S	9.0	7.3	8.6	9.5	10.1	9.6
Index of relative specific diversity D'	0.45	0.63	0.33	0.36	0.42	0.50
Index of relative phenological diversity D'_f	0.50	0.51	0.36	0.70	0.54	0.37
Relative frequency: precocious species	37.5	46.7	65.1	36.7	27.9	14.6
Relative frequencies: early species	35.1	32.1	17.4	18.8	46.5	63.5
Relative frequency: intermediate species	20.2	15.2	10.2	31.3	23.7	19.1
Relative frequency: late species	6.5	6.1	7.3	13.3	2.5	2.8

TABLE 7. Association between maximum relative frequency of each phenological group of perennial grasses in the seasonal savannas of the western Venezuelan llanos and the minimum depth attained by the water table during the rainy season

	Minimum depth of water table during the rainy season			
	Beyond grasses roots	100–150 cm		50–100 cm
Soil series	Q_{iv} Boconoito	Barinas	Camoruco	Garza
Phenological group	Precocious	Late	Intermediate	Early

Table 7 summarizes this ecological behaviour. If the five savanna communities sampled in the western llanos are disposed along a moisture gradient from the savannas with less soil water available during the rainy season (Q_{iv}) to that with the best soil conditions during this season (Garza), the four phenological groups dispose themselves along this environmental gradient from the precocious species that reach their highest frequency on the driest sites passing through the late- and intermediate-blooming groups to the early blooming species that reach their heighest frequency in the moister sites.

If the correlations between frequencies of different phenological groups are examined in the fifty samples of the western llanos, the following additional features become evident:

(1) Precocious and early blooming species, as well as early and late-blooming species, are inversely correlated. The other combinations do not show any correlation with each other.

(2) Under more homogeneous soil and habitat conditions, that is, comparing the samples within each soil series, precocious and early blooming species sharply exclude each other. The same is true for precocious and intermediate grasses.

Discussion

Let us start with the basic principle that any savanna species would do better under the most suitable environmental conditions it could meet within the whole range of habitats occupied by this type of ecosystem. That is, in our case, in sites with relatively high rainfall, a long rainy season lasting from April to November, and deep soils where water would be available during the entire growth and active period. Only when excluded from these sites by competition with other species utilizing more ably the same limiting resources, will it become cantonned into poorer and less advantageous habitats. With this premise in mind, several conclusions about the behaviour of each phenological group and of the whole ecosystem may follow from our aforementioned results.

First, the precocious species do better, in comparative terms, in sites with heavy rainfall where the rainy season already starts in April, and on deep soils with high water-storage capacity. Thus, these species are much better represented in the savannas of the western llanos than in other drier regions of Venezuela (Tables 5 and 7). But within habitats showing these favourable conditions precocious grasses occupy preferentially the driest soils. Apparently, their behaviour allows an efficient utilization of water when it is available in the soil (humid climate and deep soils), being relatively high water demanders during their growth period, since they avoid shallow, everdry soils. Because of their very early growth and sexual reproduction, these species need water as soon as the rainy season begins. This water resource does exist during the rainy season in deep, well-drained soils, but it does not arise from a seasonally high water table since the precocious species tend to disappear when the water table approaches the soil surface, such as is the case in the soils of the Garza series.

Second, the intermediate grasses behave in exactly the opposite way, since they become more important under the apparently less favourable conditions, that is, in the climatically drier sites and on shallow soils. This may suggest that the intermediate group is less competitive under conditions or irregular water supply, such as those occurring at

the beginning of the rainy season, being on the contrary highly successful where other phenological groups become handicapped by a too-short growing season. In fact, the intermediate-blooming grasses accomplish most of their vegetative development and they flourish during the peak of the rainy season, behaving thus as drought-avoiding species. Furthermore, as they develop a relatively important biomass during a short growing season, their growth-rates have to be higher than those of precocious and early growing grasses.

Third, the other two phenological groups show a transitional behaviour between the two previously considered groups. The early blooming species do better on deep soils, but in sites with a short rainy season (dry Aprils and Novembers), while the late-blooming grasses increase in frequency with total rainfall and with a more extended rainy season, but seem to perform better on shallow soils. We may predict, then, that the early blooming grasses would have a poorer effeciency in water use since they start growing just when the rains become surer and more important in amount, being thus high water demanders and drought-avoiders. On the other side, these species would be more frequent and successful on the seasonal savannas than the precocious and late-blooming ones, since a short rainy season is more frequent in savanna areas than a more extended one. Because of this adaptation to grow later in the rainy season, early and intermediate-growing grasses are the dominant species in most seasonal savannas in Venezuela.

Late-blooming grasses may profit from an extended rainy season, being in fact the sole phenological group whose frequency is tightly correlated with total rainfall and with November rains. But as they occur more frequently on shallow soils than on deep ones, we may expect that they would be poorer competitors under moist conditions while fairly tolerant of dry soils, using water when it is available after a rain.

Furthermore, from the behaviour of grass species in the savannas of the western llanos, the inference could be made that the precocious group prefers deep soils (Q_{iv} and Boconoito), where enough water is available to deep-rooted plants, but where a seasonal water table does not occur or is far beyond the reach of grasses. Late species also avoid sites with a seasonally high water table, though they do better in medium-textured soils with a higher water retention capacity (Barinas). Intermediate grasses have a similar behaviour, though they seem to be more tolerant to seasonally high water tables, while the early grasses clearly increase in frequency on these soils (Garza) where an extra water supply is available during the rainy season (Table 7). These latter are by the way the most extreme conditions of soil water saturation a seasonal savanna ecosystem can withstand, since if the water table level becomes still higher, saturating the whole soil profile, this ecosystem becomes replaced by hyperseasonal savannas.

These few conclusions suggest that each of the four phenological groups of perennial savanna grasses behave as a characteristic species guild (Root, 1968). According to this author, a guild is 'a group of species that exploit the same resources in a similar manner'. Bratton (1976) in her analysis of the understory herb community of a temperate forest, demonstrates how various temporal guilds co-occur, being responsible together with microtopography, 'for much of the niche differentiation between the herbs and thus largely account for the species diversity of this rich herb stratum'. In a similar way, the savanna grass community may partition the resources along both temporal and topography–climate axis. One temporal guild, the precocious species, becomes dominant in relatively rainy sites where the rainy season already starts in April and on deep soils with available water from the onset of rains; the other group, the intermediate-blooming, is relegated to the worst conditions: shallow soils and drier sites, but their strategy is the more secure and conservative, since they rely on the sure water resources available during the peak of the rainy season. The other two guilds segregate according to soil and rains, the late-blooming needs a moist and extended rainy season but tolerates dry soils, whereas the early blooming guild appears more competitive on deep soils but accommodates to a shorter rainy season. Fig. 5 summarizes this differential behaviour and hypothesizes certain ecophysiological
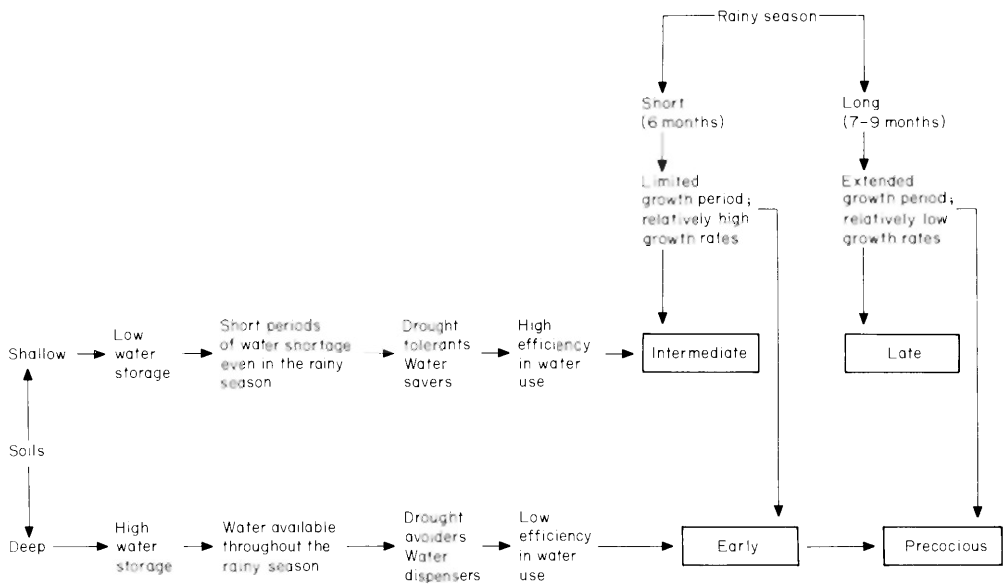
FIG. 5. Some relations between environmental pressures and plant strategies that may explain niche partition among phenological groups of perennial grasses in tropical seasonal savannas.

traits that could be associated with each strategy, though obviously these hypotheses have to be subjected to empirical proof.

Grubb (1977) and Werner (1979) discuss various mechanisms that may reduce competition and explain patterns of coexistence of species in a given community. They include differences in life-form and life-history, environmental fluctuations and phenological separation. In the case of the perennial grass community of seasonal savannas, since these species are fairly similar in life-form but differ in phenological behaviour, their annual phenodynamics will certainly contribute to niche separation. But erratic or aperiodical fluctuations in the environment have also to be kept in mind as a selective force promoting diversity.

Besides differences in growth-rate and reproductive timing, perennial grasses certainly differ in many important features related to their reproductive niche. Silva & Ataroff (1983) have undertaken the study of these reproductive and recruitment characteristics in six coexisting perennial grasses in a seasonal savanna of the Venezuelan western llanos. Their first results on reproductive effort, seed number and characteristics, seed bank, seedling survival, and plant longevity,

reinforce the picture of temporal life-history diversification as key factors explaining niche partition.

Whatever could be the environmental conditions where a given seasonal savanna community does occur, it seems important to emphasize that both high specific and high phenological diversities are constant features of all these communities. This fact implies that under any set of external conditions met with by this type of ecosystem, any one of the four types of phenological behaviour is possible and does in fact occur, quite exceptional being the exclusion of one of these groups and still rare the total predominance of one of them (but in these rare cases the two groups always persisting under whichever conditions are the early and the intermediate-blooming species). It may be suggested then that this diversity allows a rapid response to unpredictable interannual variations in rainfall or in extension of the rainy season, conditions that are indeed frequently met with in most savanna areas, where fairly dry or abnormally wet years are not unusual. Moreover, we may certainly expect that environmental variability should be one of the major factors maintaining a high diversity in the savanna grass flora. In

fact, though we do not have quantitative data on the behaviour of savanna grasses during several consecutive years, our field experience with this ecosystem supports the view that changes in relative abundance of perennial grasses are usual in tropical savannas.

Besides climatic fluctuations, the other single external pulsation seeming to affect most strongly the relative equilibrium between savanna species is the frequency and timing of fires. On the basis of available data, it is not possible yet to obtain precise indications on the influence of recurrent fires on species composition. In our analysis, with a couple of exceptions, all samples correspond to savannas burned once a year for many consecutive years. The date of burning mostly depends on the precise rain schedule in each year, since fire promotes grass growth and thus increases the forage available for cattle, and this availability that induces the owner to burn the grassland depends on rains in the preceding and in the actual year. Natural fires, on the other side, though mostly occurring in the dry season when most fuel accumulates, are also hazardous and erratic. Thus, the relative unpredictability of fire would be a strong selective pressure maintaining high specific and phenological diversity in seasonal savannas. Grubb *et al.* (1982) believe that periodic disturbance and the reactions of various species to it contribute significantly to the determination of relative abundances. In this sense, recurrent fire is a periodic disturbance that has modelled tropical savannas and their floras throughout their history.

Lemon (1949) shows some changes induced by fire in a fire-tolerant ecosystem: a pine savanna in southeastern United States. In this community, the relative abundance of different herbaceous understory species changes with time after the last burning. This layer seems to reach a relative equilibrium after about 8–10 years following burning. In Venezuela, a seasonal savanna excluded from burning for several years shows tremendous changes, both in total floristic composition and in relative abundance of the perennial grasses. According to our preliminary unpublished data from one of such protected savannas, in the Los Llanos Biological Station, it suffered notorious changes from 1967, when

we made an exhaustive sampling (Sarmiento & Monasterio, 1969), to 1981, after almost 20 years of fire protection. One of the most conspicuous changes was the decrease in diversity, both specific and phenological, with an apparent shift towards the dominance of a single early blooming grass: *Axonopus canescens*. These observations seem to confirm the important role played by recurrent burning in the maintenance of diversity in savanna ecosystems. Lemon (1949) also remarks that 'protection causes the ground cover (of pine woodlands) to become very grazy whereas burning brings about more variety in the vegetation'. It may be expected that grazing could also play a role in the tropical grassland diversity, though relevant field data concerning its action is lacking in our sampling because most Venezuelan savannas have been subjected for many years to some form of intensive cattle grazing.

To conclude, the picture emerging from this study of the seasonal savanna ecosystem as it occurs under a wide set of environmental conditions in Venezuela, is one of a well-balanced community having many coexisting grass species that are roughly similar in growth-form but conspicuously different in phenological strategies. These specific and phenological diversities may allow rapid responses to changing conditions and periodical disturbance, thus providing the ecosystem with high homeostasis. Moreover, some key external pressures, such as periods of water availability or total water storage capacity, clearly influence relative abundance of each grass species and of each phenological group, but they do not lead to a complete exclusion of any temporal guild. The major trend under any given condition is to maintain a rather high diversity within the grass community that might permit a rapid adaptation to unpredictable but recurrent disturbances both natural or man-made. This flexibility in the total grass community may also explain the dominance of the perennial grass life-form in all seasonal savanna ecosystems.

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