

The savannas of northern South America: a steady state regulated by water–fire interactions on a background of low nutrient availability

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Abstract. Savannas in northern South America (the Orinoco Llanos) are found on a variety of highly leached substrates, from tertiary sediments to alluvial soils, with markedly seasonal rainfall, 800–2500 mm/year. Physiognomic types range from tree-less grasslands to woodland type communities. Dominant tree species are evergreen and sclerophyllous being favoured by low soil fertility and fire against deciduous, mesophyllous trees. Water appears not to be a limiting factor for established trees since leaf flushing and flowering take place in the dry season.

Tree/grass ratios increase with soil water availability during the dry season. Areas with high water table, or in which a large fraction of the previous rainfall is accessible to tree roots, have higher tree densities than savannas with soils of low water retention capacity and/or deep water tables. Tree recruitment is dependent on their capability to withstand grass-root competition during early growth stages, and to reach deeper soil layers to guarantee water availability during dry periods. Therefore tree seedling establishment appears associated with flush germination during sequences of humid years. Duration of the season with plant available moisture in any year determines the productivity of the herbaceous layer, particularly the perennial grasses. The establishment of perennial grass

seedlings depends on the length of PAM and is closely related to the phenological pattern of the species.

The duration of PAM regulates specific and phenological diversity of the grass layer. An extension of the dry season may impair populations of early growers, whereas an early end of the rainy season affects negatively late species. These effects are both direct, and are mediated by species competitive interactions. Longer PAM periods determine higher probability for successful growth and reproduction of annual species.

Regular occurrence of fire determines low diversity of the tree layer and may affect its productivity if it occurs after leaf flushing and the initiation of flowering. Fire also appears to maintain vigour of the herbaceous layer, its exclusion leading to deleterious changes. Fire frequency is also associated with length of PAM. The interplay of dry, fire prone years, and wet, fireless years probably determines short-term changes in the composition of the herbaceous layer. Grass productivity is enhanced by fire during the middle of the rainy season, when there is still some water left in the upper soil layers, and the rainy season begins before water reserves are exhausted.

Key words. Fertility, productivity, water relations, phenology, architecture, Llanos, South America.

INTRODUCTION

The Orinoco Savannas (Llanos) are located in a large geosyncline in northern South America, limited by the Guiana shield to the south, the Andean Cordillera to the West and the coastal Caribbean Cordillera to the north. This region from the Guaviare river in Columbia to the eastern coast of Venezuela comprises around 500,000 km² dominated by savannas (Beard, 1953; Blydenstein, 1967; Sarmiento, 1983a). Areas of savannas are also found in the Guayana region of Venezuela.

As typical savannas, the Llanos have a characteristic physiognomy combining an open tree layer and a continuous herbaceous layer. The latter is largely dominated by the

graminoid growth form (grasses and sedges). Trees are of low stature, with rather narrow and tortuously branched stems. The relative density of trees varies widely from the tree-less savanna grassland to the savanna woodland with a 15–80% tree cover (Blydenstein, 1962; Hueck, 1971; Sarmiento, 1984). (Fig. 1). The herbaceous layer varies also considerably in density, in extreme cases with less than 50% cover, leaving large areas of bare ground. It is known that phenology, biomass allocation and production patterns of these savanna components are fundamentally different, strongly suggesting divergent strategies in the exploitation of environmental resources. Graminoid species, with an intensive root system, exploit the upper soil layers and strictly follow a growth cycle associated with seasonality of

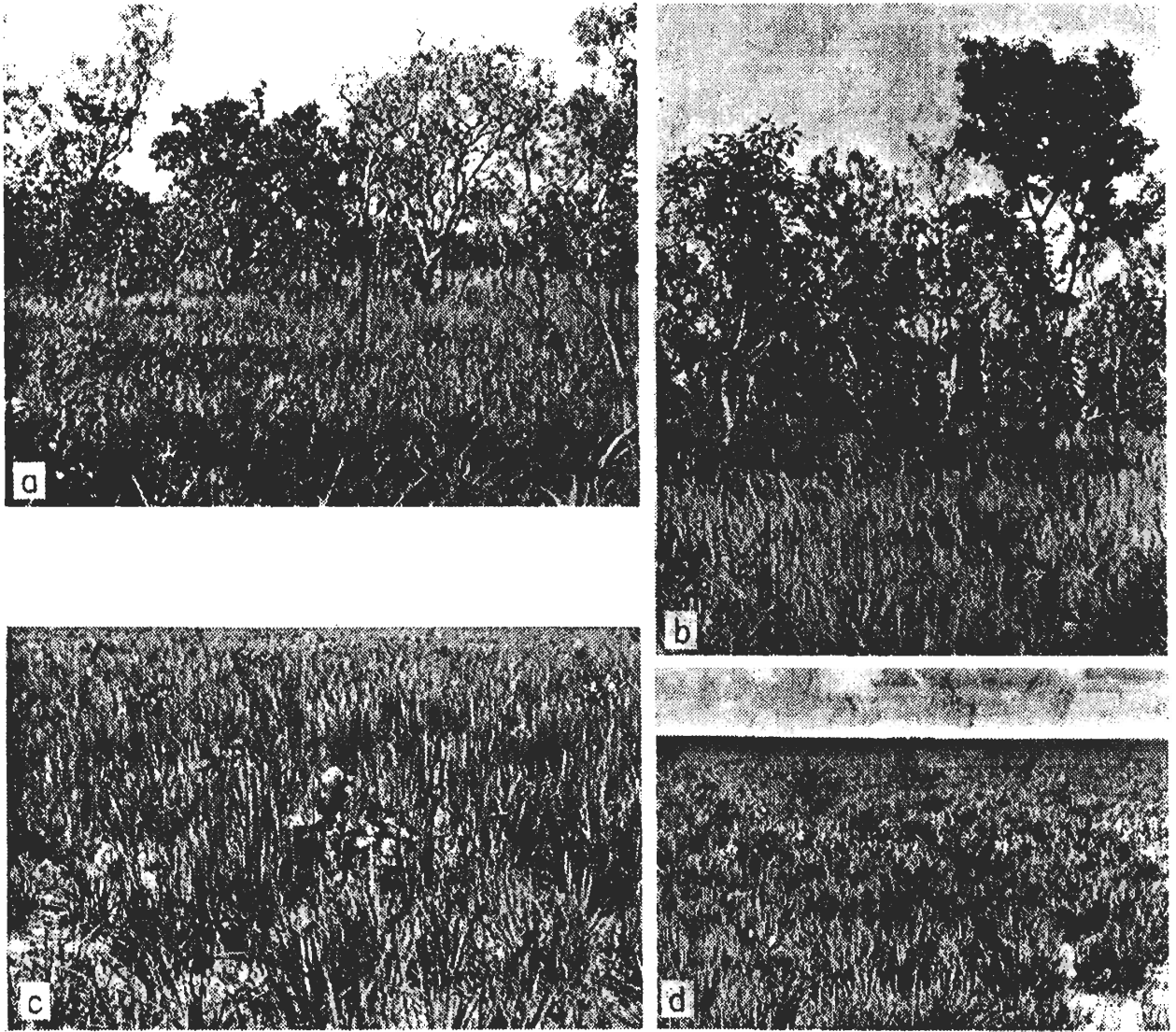


FIG. 1. Savannas in the Llanos. (a) Dense tree-savanna on clay-sandy, acid soils. The trees are *Curatella americana* (centre) and *Bowdichia virgilioides*, the tallest tree being c. 5 m. The grass layer is dominated by *Thrasya petrosa*, *Trachypogon plumosus* and *Axonopus purpusii*. 50 km south of El Tinaco, Edo. Cojedes, on the road to El Baul. Beginning of dry season, November 1989. (b) Same site and time. In the centre, *Curatella americana* (barely visible senescing leaves), left *Byrsonima crassifolia* (new foliage), and *Bowdichia virgilioides* (new foliage). Note the white inflorescences of *Thrasya petrosa* in the grasslayer. (c) Same location as (d), detail. Dwarf *Curatella americana* and bare soil patches between grass tufts (grass layer c. 60 cm high). (d) *Trachypogon*-savanna, dominated by *Trachypogon plumosus*, with scattered dwarf trees of *Curatella americana* and *Byrsonima crassifolia*. General view, in the eastern savanna of Venezuela, near Chaguaramas, c. 150 km south of Maturin. On sandy, deep soils, with very low levels of organic matter. January 1990.

rainfall, while trees, with extensive, less efficient root systems, are able to exploit both water and nutrients from deeper soil layers. As a result they show a growth cycle dissociated from the availability of rain water (Walter, 1973; Walker & Noy-Meir, 1982; Medina, 1982b; Sarmiento & Monasterio, 1983; Sarmiento, Goldstein & Meinzer, 1985).

Physiognomy, phenology, and patterns of resource utilization of savanna vegetation result from complex environmental-biological interactions. These interactions may be understood from the conceptual model put forward by RSSD program (Frost *et al.*, 1986) which consider plant available moisture (PAM) and nutrients (AN) as basic

determining factors. Performance of savannas within a given area of this plane (the PAM-AN plane) is modulated by the recurrence of fire and the frequency and intensity of herbivory.

Regional studies have emphasized the relationships between savanna physiognomy and the operating geomorphological and edaphic processes (FAO, 1965; Goosen, 1971; Cochrane & Sánchez, 1981; Sarmiento, Monasterio & Silva, 1971; Sarmiento, 1983a). In some large areas the homogeneity of geomorphological and pedogenetic processes result in a particular savanna physiognomy, such as in the tree-less savannas of the eastern plateaus of the

Orinoco Llanos and in the alluvial plains of the Apure region. In other cases, an intricate pattern of land forms results in a mosaic of savanna physiognomies, such as in the piedmont savannas of western Venezuela (Sarmiento *et al.*, 1971; Silva, Monasterio & Sarmiento, 1971). Landscape characteristics influence development of savanna vegetation by affecting basic nutrient availability (geological origin and degree of nutrient leaching) and water availability through variations in drainage and soil water retention capacity. However, the interplay of these variables has been explicitly established only on a general basis. Savanna soils appear to regulate primary production potential because of their low natural fertility, but also their texture and depth frequently affect water availability and duration of the growing period. Soil water retention capacity may exacerbate drought stress during period of low rainfall (in sandy soils) or increase the extent and intensity of flooding in heavy soils during the peak of the rainfall season.

The main aspects of phenology, water relations and nutrient economy, in connection with productive processes in neotropical savannas have been reviewed recently (Cole, 1986; Medina, 1982a, b; 1987; Sarmiento, 1983a; 1984; Tohill, 1985). Therefore, in this paper we will concentrate on the problem of coexistence, and variations in densities, of trees and grasses. Our point of view is that the Orinoco savanna soils have a widespread low fertility status, therefore patterns of variation in ecosystem structure and productivity are more correlated with the duration of plant available moisture and the frequency and timing of fire. In addition, the phenological and architectural characteristics of savanna plants play a significant role in determining responses to environmental stresses.

ENVIRONMENTAL FRAMEWORK AND ECOSYSTEM PROCESSES

Water availability and savanna physiognomy

There are few studies on the geographic variation of annual rainfall in the savannas area of northern South America (Burgos, 1967; Walter & Medina, 1971; Sánchez & García, 1969). Total rainfall varies widely, and ranges from 800 to 2500 mm being concentrated in a wet season of 5–8 months duration (Monasterio, 1970; Susach, 1984). Mean annual rainfall is frequently correlated with the length of the rainy season and the number of rainy days, as in several other areas in the tropics (Medina, 1986).

The range of savanna types found within the Orinoco Llanos (seasonal, semi-seasonal, and hyperseasonal; Sarmiento & Monasterio, 1975) and their structural and floristic variations appear to be regulated by a combination of soil properties and rainfall patterns. As pointed out above, trees and herbs have different rooting patterns. Therefore, in what follows we will consider top soil characteristics to refer to the grass component responses, while deeper soil layers will be taken into account for the woody components.

Texture, structure, depth of profile, relative topography, and slope control drainage and water storage capacity of

soils under a strongly seasonal rainfall distribution (Silva & Sarmiento, 1976). Variations in total annual rainfall have different effects depending on soil properties. Higher annual rainfall favours the growth of plants adapted to flooding but is deleterious to seasonal savanna species. In savannas with good water storage capacity and moderate to good drainage, increases in annual rainfall lengthens period when PAM is sufficient for growth. This effect is less pronounced in soils with lower water storage capacity and good to excessive drainage, where the length of PAM is shorter. The relationship between water availability and grass production may be demonstrated experimentally extending the PAM period. Natural *Trachypogon* grasslands irrigated during the dry season are able to maintain a green biomass similar to that of the rainy season, indicating that there is no intrinsic seasonal reduction in grass growth capability (San José & Medina, 1976).

Established trees can use underground water during the dry season; therefore, they are not affected by the length of the period when PAM in the upper soil layers is sufficient for growth. We assume that annual rainfall, depth of permeable substrate and drainage regulate tree density in these savannas. Deep permeable substrates result in a water table beyond the reach of tree roots, and therefore in a grassland savanna physiognomy. At the other extreme, a superficial impervious layer (f.i. lithoplinthic hardpans) does not allow tree root development, and again the result is a tree-less grassland. In high rainfall areas with poorly drained soils (seasonal floods), or in low rainfall areas with very permeable soils (longer dry seasons) we also find grasslands. In moderately drained soils increased rainfall leads to higher tree densities (woodlands).

Trees develop new leaves and flower between the middle and the end of the dry season (Foldats & Rutkis, 1975; Monasterio & Sarmiento, 1976). During this season new leaves show moderate photosynthetic rates and pronounced water losses through transpiration (Vareschi, 1960; Foldats & Rutkis, 1975; Sarmiento *et al.*, 1985). This behaviour indicates that roots of savanna trees have free access to water from moderately deep soil layers; however, stomatal conductance is reduced by the lower air water vapour partial pressure during the dry season. Reduction of transpiration due to lower stomatal conductance seems to be compensated by the increased leaf-air water pressure deficit during the dry season (Medina, 1982a; Sarmiento *et al.*, 1985). The development of large leaves under the high radiation, high temperature environment characteristic of the Orinoco savannas is also a clear indication that the energy balance of the leaves is guaranteed by sufficient water availability allowing evaporative leaf cooling. However, it seems that leaves produced during the dry season have smaller areas than those which grow after the onset of rains (Montes & Medina, 1977).

There is virtually no information on the physiological characteristics of tree seedlings, in regards to their growth rates and resistance to water stress. However, tree seedling establishment appears to be heavily constrained by grass root competition and risks of drought and fire. Survival of tree seedlings generated during a given rainy season depend on the water availability in the top soil

the domain of the herbaceous layer roots. Probability of seedling establishment depends on their capability to reach moist soil layers beyond the grass root zone, and on the build up of underground energy reserves which allow regrowth of aerial biomass after fire or drought. We expect this probability to be directly correlated with the length of the rainy season. Moderately drained soils with medium to high water tables and long rainy seasons result in higher recruitment and therefore higher tree densities. Towards shorter average PAM lengths, recruitment would depend on the occurrence of flush germination taking place during wetter years of lower mortality. During average or drier years, only well established trees would persist.

From these considerations it is concluded that the evaluation of the water availability in the Orinoco savannas has to take into account both climatic and edaphic parameters. Ideally soil water availability should be measured directly at different soil depths, to include the whole rooting zone. This type of measurement has been conducted by San José & Medina (1975) and Sarmiento & Vera (1977) for savannas in Central and Western Venezuela, respectively. These estimations require frequent periodic measurements of soil conductivity (or neutron radiation absorption), which have to be calibrated against gravimetric determinations of soil water content. This may be the reason why this type of data is so scanty in the savanna literature. Climatological approaches have been frequently utilized to measure PAM in several tropical regions with different degrees of success (Lal, 1987). Lack of agreement with vegetation performance derive from the fact that climatological measurements of PAM frequently do not take into account the soil properties in a given area. An approach to solve this problem would be to consider the limit between dry and humid seasons, calculated by any of the different methods available in the literature (Lal, 1987), as representative for soils of moderate drainage. Differences in texture can be taken into account allowing a given percentage of variation around the average climatological figure. We have done that with a particularly simple moisture index based on average rainfall and temperature data proposed by Bailey (1979). A number of savanna meteorological stations covering the range of rainfall in the Orinoco Llanos show variations of average periods when PAM is sufficient for growth from 150 to 229 days, but average extremes span from 128 to 251 days (Table 1). There is a reasonable degree of agreement of established PAM length with meteorological data and those estimated through direct and frequent measurements of soil water content, considering that the mean meteorological index has been calculated on the basis of average rainfall and temperature (Table 2).

Nutrient availability and productivity of savannas in the Llanos

Tropical savanna soils in northern South America can be considered homogeneously dystrophic because of their geologic origin and the leaching effect of relatively high rainfall (Blydenstein, 1967; Sarmiento, 1984; Cole, 1986). Therefore, it is expected that variations in actual organic matter production are probably less related to the fertility

TABLE 1. Average duration of the growing season (PAM length in days) in Orinoco savannas with contrasting annual rainfall. Calculated on the basis of the monthly Bailey index* allowing 20% variation in rainfall/evaporation ratio due to soil texture and water retention capacity.

Station	Annual rainfall	Beginning	End	Duration	Average extremes
Puerto Ayacucho	2144	27 April	11 Dec.	229	214-251
Caicara	1526	8 May	2 Nov.	178	167-193
Barinas	1400	22 April	3 Dec.	225	211-240
Calabozo	1239	13 May	19 Nov.	190	177-207
Valle de la Pascua	1025	25 May	22 Sept.	150	128-173

*Bailey index $si=0.018 P/1.045T$; the value for rainfall/evaporation balance is 6.37 on a year basis and 0.53 on a monthly basis.

status of the soils than to other factors such as water availability and fire regime. Evaluation of soil fertility status has been a matter of debate because of disagreements on how to compare soils with different proportion of fertility factors such as organic matter, nitrogen, and phosphorous content, sum of bases; pH and Aluminum mobility (Medina, 1988). Often fertility status of savanna soils has been evaluated on the basis of analyses of the upper soil layers, which are obviously of more interest for agricultural purposes, but may bear little relation with the development of natural vegetation. It seems that a useful index for the estimation of the fertility status of savanna soils is the sum of bases, which allow the separation of dystrophic, mesotrophic and eutrophic soils (Huntley, 1982; Sarmiento, 1990). This criterion is acceptable provided that an agreement is reached on the methodology for its measurement, particularly the cation extraction procedures and the determination of the cation exchange capacity. On the other hand, care should be taken to sample soil profiles beyond the grass root zone, because upper soil layers are strongly affected by the process of organic matter production of the grass cover. This last statement may be visualized using the

TABLE 2. Comparison of PAM length based on direct soil water content measurements and on the Bailey moisture index calculated with long-term average rainfall and temperature data (Bailey, 1979).

Station	Estimated PAM duration (days)		
	Soil water content	Monthly Bailey index	
		Average	Extremes
Gurza*	270		
Barinas*	239	225	211-240
Bojonoito*	225		
Calabozot	222	190	177-207

*Soil depth 100 cm (Sarmiento & Vera, 1977).

†Soil depth 70 cm (San José & Medina, 1975).

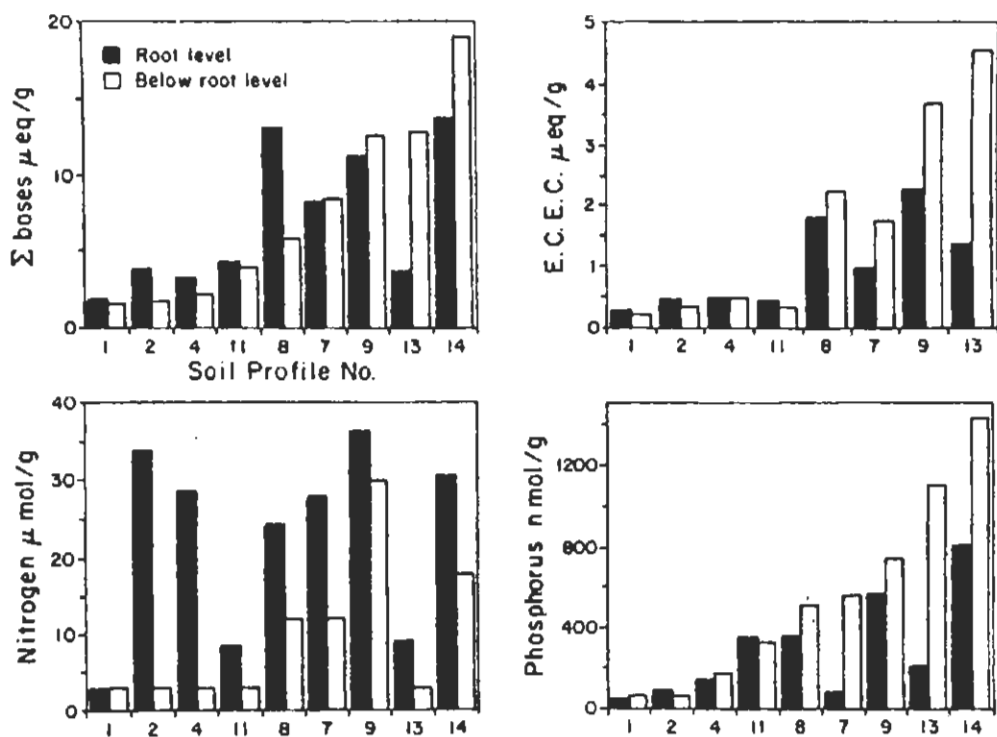


FIG. 2. Fertility factors in savanna soils. Analyses differentiate among soil properties at the root level and below the root level in each savanna (original data from Susach, 1984). Soil profiles are ordered according to increasing Σ bases in the soil layer below the root level. Soil profile number indicate soil pits with the following classification: Profile 1: Typic quartzsamtment. *Trachypogon plumosus* (H & B) Nees.+trees; root depth 45 cm; Profile 2: Undefined. *T. plumosus* (H & B) Nees., tree-less; root depth 30 cm; Profile 4: Aquic quartzsamtment. *T. plumosus* (H & B) Nees., tree-less; root depth 70 cm; Profile 7: Aeric tropaqualf. *T. plumosus* (H & B) Nees.+ trees; root depth 40 cm; Profile 8: Oxic paleustult. *T. vestitus* Anders.+ trees; root depth 18 cm; Profile 9: Typic plinthaqualf. *T. plumosus* (H & B) Nees.+ *T. vestitus*, tree-less; root depth 30 cm; Profile 11: Oxic rhodustalf. *T. plumosus* (H & B) Nees.+ trees; root depth 110 cm; Profile 13: Lithoplinthic ustorthent. *T. vestitus* Anders.+ *Byrsonima verbascifolia* (L.) H.B.K.; root depth 45 cm; Profile 14: Typic tropaqualf. *Axonopus anceps* (Mez.) Hitchc., tree-less; hyperseasonal; root depth 35 cm.

detailed soil analyses performed by Susach (1984) in his study of grassland productivity in Orinoco savannas in the southern Guárico State in Venezuela (Fig. 2). It is clear that soil characteristics within the grass root layer are strongly affected by plant activity, thereby obscuring the true nutrient status of the soils considered. Notice that soil N content is always higher within the root zone than below, while these relationships are not so clear with extractable P. Availability of P is the other nutrient appearing to be limiting natural savanna productive potential. Interestingly, extractable P in this soil sample set is significantly correlated with the sum of bases, but the coefficient of determination is far stronger for the soil layer immediately below the root level ($r^2=0.606$ at the root level, and $r^2=0.957$ below the root level). These relationships should be further investigated to develop a robust soil fertility index for natural savannas.

In Brazilian savannas variations in tree densities have been associated with the nutritional capacity of the soils, particularly P deficiency and associated Al mobility (Goodland & Pollard, 1973; Lopes & Cox, 1977). Open grasslands (campos limpos) are supposed to grow on soils with higher Al/Ca ratios than those of dense woodlands (Cerradão) or the semi-deciduous forest found in the Brazil-

ian Cerrado areas. Doubts on these soil-vegetation correlations have been raised because soil samplings was made within those soil layers directly influenced by the vegetation (Medina, 1982b; Montgomery & Askew, 1983). Nevertheless, high Al mobility in many South American soils in contrast to Australian and African soils (Sánchez & Isbell, 1978) may play an important role in selecting plant species which resist Al toxicity either through exclusion at the root level or detoxifying it after uptake (Medina, 1982b; Haridasan, 1987). Nutrient availability certainly regulates grassland aboveground biomass production, and overall P deficiency has been clearly demonstrated for both native and introduced pastures in the Orinoco Llanos (Medina, Mendoza & Montes, 1978; San José & García-Miragaya, 1981). Nitrogen availability seems to be limited both by the accumulated pool in the soil and its rate of mineralization, and its deficiency may be aggravated by the recurrence of fire (Medina, 1982a, 1987).

There are not enough productivity data of savannas in the Llanos to establish if variability of production values obtained in different sites can be accounted for by differences in soil nutrient availability. Rather, variations in aboveground biomass accumulation have been often associated with interannual variations in the length of

TABLE 3. Soil fertility (Σ bases below root level), duration of PAM and maximum aboveground biomass accumulation in regularly burnt seasonal and semi-seasonal savannas.

Savanna site	Σ bases ($\mu\text{eq/g}$)	Estimated PAM duration (days)	Aboveground production (g/m^2 year)	
Boconoito (ultic haplustalf)	1.5	211	534	(1)
Puerto Ayacucho (typic ustipsamment)	3.6	214	393	(3)
Calabozo		190	198-635	(4)
Barinas (oxic paleustalf)	6.3	228	590	(1)
Cabruta (1) (quartzipsamment)	6.5	167	178-288	(2)
Garza (oxic paleustalf)	10.7	225	604	(1)
Cabruta (2) (typic tropaqualf)	19.0	167	688	(2)

(1) Sarmiento & Vera, 1979; Sarmiento, 1984; (2) Susach, 1984; (3) Guinand & Sánchez, 1979, with soil data from Blancaneux, Hernández & Arango, 1977; San José & Medina, 1975, 1976; Medina *et al.*, 1978.

PAM. In addition, lack of reliable data on underground biomass production prevents any definitive conclusion at this time. Some examples obtained in different savannas in Venezuela (Table 3) indicate that dense swards are produced in relatively richer soils with short lengths of PAM (Cabruta 2) as well as in poorer soils with longer lengths of PAM (Barinas). In a given savanna a wide range of values of aboveground biomass production have been measured in different years (Calabozo). The sum of bases for the savannas included, however, show that all sites are extremely low in nutrient availability (Montgomery & Askew, 1983).

Fire effects

✧ Regular occurrence of fire selects those tree species that resist burning of aboveground biomass. Areas protected against fire for more than 20 years show a significant increase in tree density, both of fire-resistant common savanna species, and fire susceptible species from the surrounding semi-deciduous forest (San José & Fariñas 1983). The number of tree species and stem density appears to be increasing quite rapidly in the last 6 years of protection (Fariñas & San José, 1987) (Table 4).

✧ These data suggest that the predominance of evergreen trees, characteristic for neotropical savannas, is related to their fire resistance. Deciduous trees, with phenological cycles associated with the distribution of rainfall, appear to be more fire sensitive, and are therefore excluded from the set of woody species inhabiting regularly burned savannas. This observation is relevant because the predominance of sclerophyllous, evergreen trees has been considered a con-

sequence of selection in nutrient poor environments (Montes & Medina, 1977).

Fire and water are not independent factors because probability of fire decreases with increasing lengths of the rainy season. These interactions may influence tree density as discussed above.

Fire is also an important factor of mortality in some grass species, specially those with short rhizomes close to the surface (Silva & Castro, 1988). However, the exclusion of fire leads to deleterious effects on the perennial grass layer. In the Biological Station at Calabozo, within areas protected from fire and grazing for more than 20 years, perennial grasses are dying back, leaving large patches of empty ground covered by dead plant material. Studies on the demography of perennial grasses in burned and protected plots showed that lack of fire result in higher seedling mortality, a reduction in size and vigour in adults, and a trend toward local extinction (Silva *et al.*, unpublished). The pattern of change in grassland composition after fire protection is a short term increase in diversity (after 8 years, San José & Fariñas, 1983) and a long-term reduction in the relative dominance of grasses. In these *Trachypogon*-grasslands the relative density of *Trachypogon plumosus* (H&B) Nees, was reduced from 57% at the beginning of the protection to about 14% after 20 years, while that of *Axonopus canescens* (Nees. & Trin.) Pilger increased from 16% to 44% during the first 16 years of protection, receding to 33% 6 years later (Fariñas & San José, 1987).

The case study of savanna protection against fire in Calabozo shows that the long-term accumulation of dead biomass leads to the death of the whole grass layer. The duration of the die back process may differ among species. The interplay of fire prone years, and wet, fireless years probably determines short-term changes in the composition of the herbaceous layer. Also, the patchy nature of savanna fires may result in a mosaic of savanna composition associated to slight changes in species dominance.

Burning of grasslands during the dry season results in a stimulation of the production of aerial shoots and changes in the production pattern of the sward. Accumulation of dead standing biomass and a reduction in the total amount of green foliage as the dry season approaches has been shown to be the normal pattern of biomass development in several savannas in the Llanos (San José & Medina, 1975;

TABLE 4. Number of stems/ha in a protected plot in the Biological Station at Calabozo, Edo. Guárico (Fariñas & San José, 1987).

Species	1962	1969	1977	1983
Savanna trees (evergreen)	92	174	270	1010
Forest species (evergreen)	1	3	11	32
Forest species (deciduous)	0	77	229	1319
	93	† 254	510	2361

Bulla, Miranda & Pacheco, 1980; Nazoa & López-Hernández, 1981; Susach, 1984). Several authors have shown that burning results in an increase of the aerial biomass production (Blydenstein, 1962; San José & Medina, 1975; Medina *et al.*, 1978; Guinand & Sánchez, 1979), but frequently the contrary has been observed (Blydenstein, 1962; Susach, 1984). It should be noticed that the effect of burning on aerial biomass development is different from the regrowth induced by cutting (Medina *et al.*, 1978). The reason for these contradictory results may reside in timing of burning, which is associated with the soil water availability (Medina, 1982b), and community composition. Burning too early in the dry season stimulates grass growth leading to a depletion of soil water reserves, and eventually death of the new shoots produced, thereby decreasing underground reserves for the next growth period. Burning too late in the dry season delays the process of new shoot development, resulting again in a reduction in aerial biomass production during the following rainy season. However, these responses may be modified by the phenology of the particular species involved. The pattern of root biomass production appears to be less affected by burning (Guinand & Sánchez, 1979; Susach, 1984), although in some cases positive responses to burning during the middle of the dry season have been observed (San José & Medina, 1975). There are many technical difficulties for an accurate assessment of belowground productivity in grasslands. However, the pattern of variation of total belowground biomass (including roots and rhizomes) points to a clear reduction of belowground biomass when aerial biomass is actively developing, followed by an accumulation towards the beginning of the dry season (Susach, 1984) (Fig. 3). Seasonal changes of total underground biomass are difficult to interpret, since they are the result of mortality and decomposition of old roots, translocation of nutrients and organic compounds and the development of new roots.

POPULATION DYNAMICS AND STRUCTURAL FEATURES

Variations in physiognomy and plant cover are determined by physico-chemical factors. However, we know very little as how these factors operate upon savanna structure. To understand the processes and mechanisms involved we have to consider the role of some biological properties and interactions of savanna plants. Firstly, we will refer to phenology and its role in the effects induced by rainfall regime in savannas of different composition. Then, we will consider plant architecture, its relations to phenology and to interactions between species.

Phenology

Studies on the floristical and phenological diversity of Orinoco savannas have shown that despite similarities in seasonal growth, perennial grasses show important differences in growth form and phenology, both vegetative and reproductive (Sarmiento & Monasterio, 1983). Other differences are related to their demographic properties (Silva & Ataroff, 1985). Niche differentiation along these and other axes may be responsible for specific diversity. This biological and ecological diversity seems to mediate in the changes in plant cover and biomass induced by environmental factors. Sarmiento & Monasterio (1983) described the temporal division of the niche in the grass layer of a seasonal savanna on the basis of four phenological types: precocious species which flower at the transition between the dry and the wet seasons; early species, which flower during the first 2 months of the wet season; intermediate species, flowering during mid-season months; and late species, which flower during the last 2 months of the wet season. These phenological types correspond to reproductive and vegetative endogenous rhythms of aboveground biomass. The over imposed seasonality of water affects growth on a quantitative basis and regulates the ratio of living to dead biomass.

The dynamics of the proportion and productivity of the different components of the grass layer is modulated by the on- and offset of rains and the duration of the intervening period (PAM). Sarmiento (1983b) showed that the specific diversity is significantly higher in humid savannas (>1600 mm/year) than in the dry savannas (<1100 mm/year). Also, precocious, early, and late species showed higher relative frequencies in humid savannas, whereas intermediate species showed higher relative frequencies in dry savannas.

Perennial grasses with different phenologies show very different seasonal regrowth curves (Sarmiento & Monasterio, 1983; Silva, 1983). When precocious species grow under field conditions their growth is maximum during the first 2 months of the rainy season, when the other species are still very low. When they grow alone, without neighbour interference, the growth period is longer and production higher (Gallardo, 1983; Canales and Silva, 1987; Raventos & Silva, 1988). Silva (1987) discussed the possible effects of changes in the length of the rainy season on the population dynamics of grass populations differing in both their reproductive phenology and their reliance on

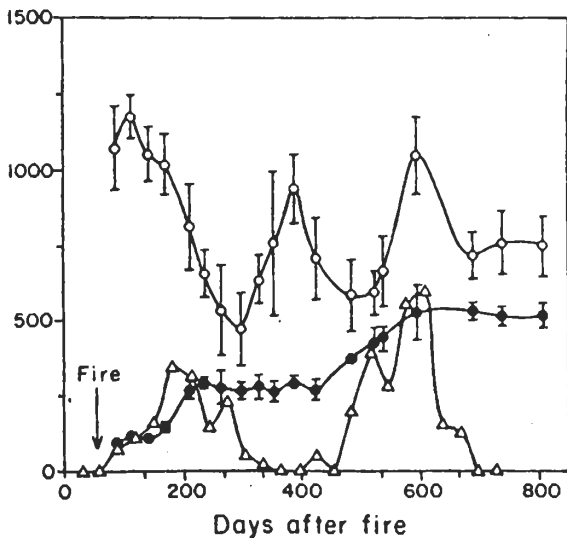


FIG. 3. Seasonal variations in above- and belowground biomass in savannas dominated by *Trachypogon plumosus* (H & B) Nees. Δ , Rainfall (mm); \circ , belowground biomass (g/m^2); \bullet , aboveground biomass (g/m^2) (data from Susach, 1984).

seed reproduction. A decrease in the length of PAM reduces the annual growth and reproduction of some phenological types without direct effects upon others. Beyond certain limits, this may not only reduce the population biomass but may result in local extinction. Other coexisting species may be benefited. In Fig. 4 we show a graphic hypothesis of the effects of changes of PAM upon the annual regrowth of the different phenological types of perennial grass species. A delay in the onset of rains, would seriously diminish the possibilities of precocious and early species to produce green foliage, since when the competitors are small water limits their growth potential and when water is available, competitors are growing fast. This affects not only their annual vegetative production but also their population recruitment since they flower very early in the wet season. By the same token, a shorter wet season (ending earlier) would affect late species since they would experience water stress during the peak of growth and reproduction. Intermediate species would not be affected by these changes and therefore they would take advantage of the decline of competitor populations (Sarmiento, 1983b).

Architecture

Plant architecture is another axis of differentiation of savanna species. It plays an important role in the interactions between plant and environment and between species, but few studies are available. Recent data (Silva,

1987, and unpublished) show that the savanna grass architecture is closely related to phenology as well as to competitive interactions between species.

A first level of relation between phenology and architecture is the pattern of underground biomass allocation. Since precocious and very early species flower and produce most of their foliage during the first 3 months of the rainy season (Fig. 4), they are expected to have underground reserves (both energy and nutrients) to sustain this rapid growth. That is, they depend on energy and nutrient accumulation from the previous growing season. The other species regrow more slowly, reaching their peaks of growth at different times later in the wet season. The longer the lag phase, the lesser would be the requirement for an underground reserve to sustain this growth because nutrients would be available from the soil and the cost of new foliage is covered by current photosynthesis. There seems to be a clear correlation between the ratio of below/aboveground biomass and flowering month as shown in Fig. 5.

Aerial architecture of perennial grasses could be classified into two general types: basal and erect plants. In the basal types, the elongated culms bear small leaves and the foliage is produced from short, basal internodes. In the erect type, elongated culms bear long leaves, and as the culm grows upwards the mass of leaf surface is displaced upwards. Precocious and early grasses show a basal architecture. For the other species, the later they flower the more erect their habit and the higher their culms (Silva, 1987). Differences in final height between species are due to the number of internodes in the culms, which are predetermined several months earlier, when the apex differentiates into inflorescence. These differences result in various patterns of vertical distribution of foliage throughout the season. In Fig. 6 we show profiles of several perennial species by the end of the growing season, ordered from precocious to late species. Basal-precocious species occupy their aerial space very rapidly whereas this process takes more time in the erect species depending on their height.

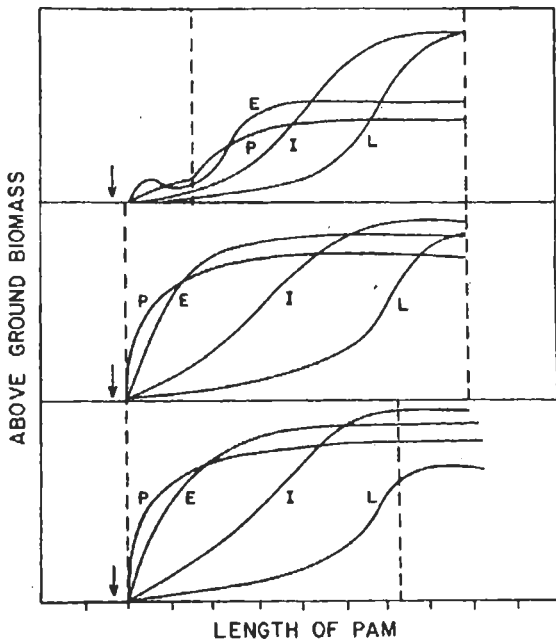


FIG. 4. Hypothetical effects of the changes in the length of PAM on the annual regrowth of aboveground biomass of different phenological types of perennial grasses (P=precocious; E=Early; I=Intermediate; L=Late). Arrows indicate the occurrence of fire. PAM length is indicated by the area between the broken lines. The middle set of curves represent a long rainy season (approx. 8 months). The upper set shows an extension of the dry season, while the lower set represents a reduction of the rainy season.

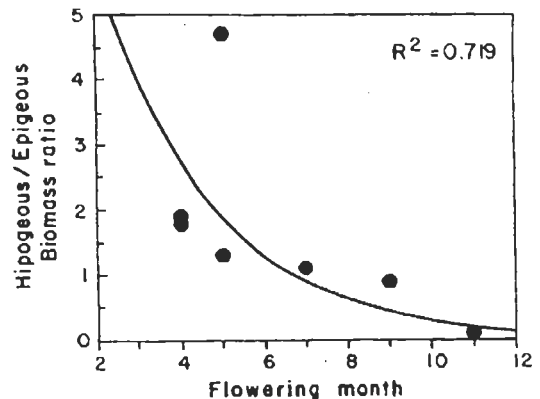


FIG. 5. Hipogeous/epigeous biomass ratios as a function of flowering time in seven perennial grass species. (Data from Sarmiento & Monasterio, 1983; Silva, unpublished.)

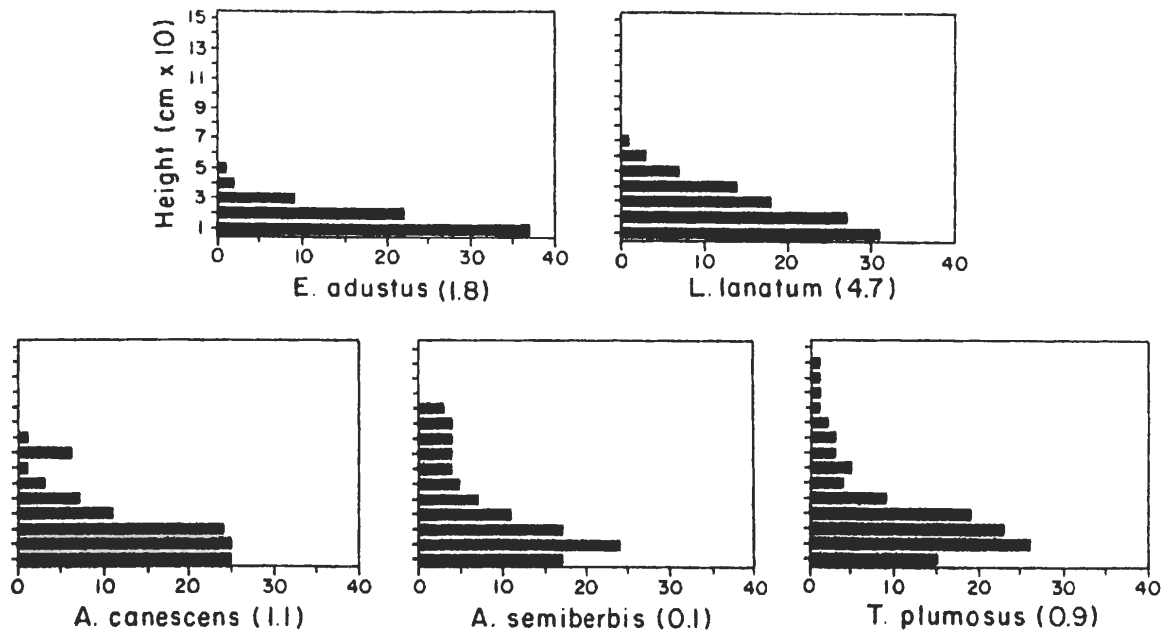


FIG. 6. Vertical distribution of aerial biomass as a percentage of total in five grass species with different flowering times: *Elyonurus adustus* (Trin.) Eckm., *Leptocoryphium lanatum* (H.B.K.) Nees., *Axonopus canescens* (Trin.) Pilger, *Andropogon semiberbis* (Nees.) Kunth, *Trachypogon plumosus* (H & B) Nees. Number in parentheses indicate hipogeous/epigeous biomass ratios. (Data from Raventos & Silva, 1988; Sarmiento, 1984.)

Relative height is important in the competitive interactions between species. In savanna grasses, taller species interfere in the growth of the lower ones more than vice versa, despite the fact that the former reach their peaks of growth later. Growing close to other species results in changes in the pattern of foliage distribution and a reduction of the season growth, in both precocious and late species. Basal species seem to have higher productive potential than taller (late growers) species but since interference from late growers is higher all types attain the same level of annual production of aboveground biomass when growing together under natural conditions (Raventos & Silva, 1988).

Annual grasses

Annual grasses constitute another component of the grass layer, being affected by changes in PAM. Common annual species belong to the genera *Andropogon*, *Aristida*, *Diectomis*, *Eragrostis* and *Gymnopogon* (Ramia, 1974; Sarmiento & Monasterio, 1983). Annual grasses share several common architectural and ecological traits. They are erect, but not taller than a few decimeters, and largely restricted to the bare ground left between the clumps of perennial grasses, where they form high density patches. They germinate as soon as rains start and grow fast during the rainy season. In contrast to the behaviour of annual grasses described for African savannas, in the Llanos annual grasses are restricted to savannas with longer PAM. Studies on the population ecology and the physiology of these annual grasses are badly needed to understand the dynamics of perennial–annual strategies in neotropical savannas.

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