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4 Biodiversity and Water Relations in Tropical Savannas
Guillermo Sarmiento

4.1 Introduction

The analysis of savanna biodiversity and the comparison of different savanna communities is difficult due to the scanty information that exists regarding several components of the biota such as microorganisms, non vascular plants, invertebrates, and even vertebrate animals. Fortunately, enough is known of the vascular flora of several savanna communities to allow some comparisons. Unfortunately, the information on the functional groups within the vascular flora from savannas is restricted to a few study sites. This chapter reviews the savanna floristic richness based on the known vascular flora; discusses several aspects of functional diversity, especially in terms of responses to water stress, and suggests some hypothesis regarding the role of PAM and other determinants.

4.2 Biodiversity of Neotropical Savannas

4.2.1 Species Diversity

It is well known that the total number of species in any plant community depends on the size of the sampled area, as shown in Table 4.1 for the vascular flora from savanna communities from Africa and South America. From this information, the variation of species richness with the sample area can be derived, as shown in Fig. 4.1, from a minimum of 10 spp./m^2 to 100 spp./ha.

Along a soil catena in the Venezuelan western Llanos (Silva and Sarmiento 1976), the mean number of vascular plants sampled in 10 x 10 m quadrats ranged from 24.5 to 35.4 (Table 4.2). The total number of species per 1000 m^2 ranges from 53 to 85, when the ten samples from each soil type are added.

Table 4.1. Floristic richness in some American and African savannas

Locality		
Lamto, Ivory Coast (1)	16 spp/m^2	20-35 spp/250 m^2
Nazinga, Burkina Faso (1)	8 spp/m^2	30-35 spp/1000 m^2
Calabozo, Venezuela (2)	15 spp/m^2	98 spp/520 m^2
Barinas, Venezuela (3)	25-35 spp/100 m^2	53-85 spp/1000 m^2

(1) Fournier (1991)
(2) Sarmiento and Monasterio (1969)
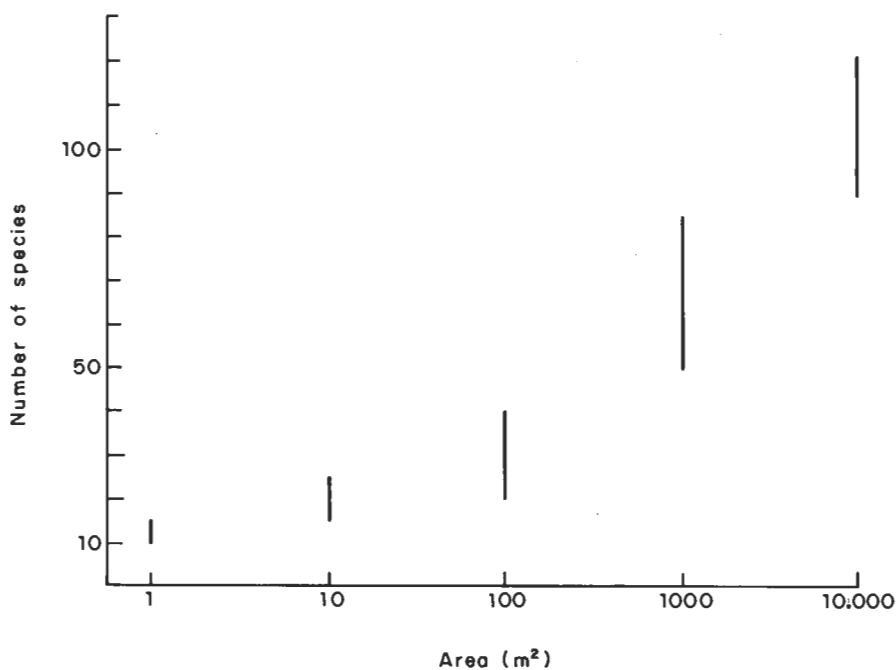(3) Silva and Sarmiento (1976)

Fig. 4.1. Total number of vascular plant species according to the area sampled in different tropical savannas. The *vertical bars* indicate the range of floristic richness for each area

Table 4.2. Floristic richness in savannas of the Venezuelan llanos. (Data from Silva and Sarmiento 1976)

Savanna community	Mean no. of plant species in 10 stands of 100 m^2	Mean no. of perennial grasses in 10 stands of 100 m^2	Total no. of plant species in 1000 m^2
Palma Sola	27.4	7.3	55
Boconoito	31.6	8.6	63
Barinas	35.1	9.5	69
Camoruco	35.4	10.1	81
Garza	34.3	9.6	85
Gásperi	27.1	10.1	75
Jaboncillo	24.5	11.6	53

Table 4.3. Floristic richness of various neotropical savanna formations. (Sarmiento 1983a)

Formation	Area (km^2)	No. of. trees and shrubs	No. of sub-shrubs, half-shrubs, herbs, vines, etc.	No. of grass species	Total no. of species
Cerradoin north-western Sao Paulo (Eiten 1963)	50	45	175	14	237
Cerrado in western Minas Gerais (Goodland 1970)	15 000	~200	~330	73	~600
Whole cerrado region (Heringer et al. 1977)	2 000 000	429 (774)	181	108	718 (1063)[a]
Rio Branco savannas (Rodriguez 1971)	40000	40	87	9	136
Rupununi savannas (Goodland 1966)	12 000	~50	291	90	431
Northern Surinam savannas (Van Donselaar 1965)	~3 000	15	213	44	272 (445)[b]
Central Venezuelan llanos (Aristeguieta 1966)	3	69 (16)[c]	175	44	288
Venezuelan llanos (Ramia 1974)	250 000	43	312	200	555
Colombian llanos (FAO 1966)	150 000	44	174	88	306

[a] Total flora including other plant formations.

[b] Total flora including bushes.

[c] Number of savanna trees excluding groves.

Considering the total vascular flora, the Brazilian cerrados are the richest neotropical savannas (Table 4.3) with more than 400 woody species and about 300 herbaceous species (Eiten 1963; Toledo Rizzini 1963; Goodland 1970; Heringer et al. 1977). Goodland (1966) reports 431 species for the Rupununi savannas in Guyana, and Van Donselaar (1965) reports 272 species for northern Surinam savannas.

In Calabozo, Venezuela, the total number of species is 288 in an area of 390 ha (Aristeguieta 1966). This figure includes the open savanna-grassland and the small isolated forest patches. The number of species in the open savanna is 175.

In West Africa, Fournier (1991) reports 130 species for the vascular flora from the Experimental Station in Lamto, Ivory Coast, and 200 species for somewhat drier savannas of Nazinga, Bourkina Faso. Floristic richness in these moist savannas seems to increase as the climate becomes drier, and this occurs in both woody and herbaceous species. In the latter, the increase is mainly due to a greater number of annual species. To the North, in the much drier Sahelian savannas from Fété Olé in Senegal, Bourlière (1978) listed 103 herbs and 22 woody species for a total of 125 vascular species.

Considering the species diversity in the grass family, the most important family of vascular plants in savannas, Sarmiento (1983b) showed that in forty 100 m^2 stands from Venezuelan savannas the number of perennial species ranged from 3 to 12, and the mean value was 7.2 species per stand.

Concerning evenness, medium values seem to be the rule in West African savannas (Fournier 1991) as well as in western Venezuelan savannas (Fariñas, pers. comm.).

The figures presented above suggest that although tropical savannas are certainly poorer in species than the humid tropical forest, they are relatively rich plant formations in the upper part of the range for terrestrial plant communities.

4.2.2   Ecological Diversity

Besides specific diversity, it would be convenient to consider other aspects of diversity such as growth forms, phenology, functional groups, and plant strategies. Tropical savannas seem to maintain rather higher levels of structural, morphological, and functional diversity. This is due to the varying proportion of woody and nonwoody elements, which results in a wide range of structural types from almost closed forest to pure grasslands. Morphological diversity is produced through the combination of the three equally important woody, half-woody, and herbaceous growth-forms. Functional diversity exists because of the coexistence of species of various types such as evergreen or deciduous, shallow or deep-rooted, perennial or annuals, and C_3 or C_4. Moreover, vegetative and reproductive phenologies show a wide range of annual patterns; some species grow only during the wet season,
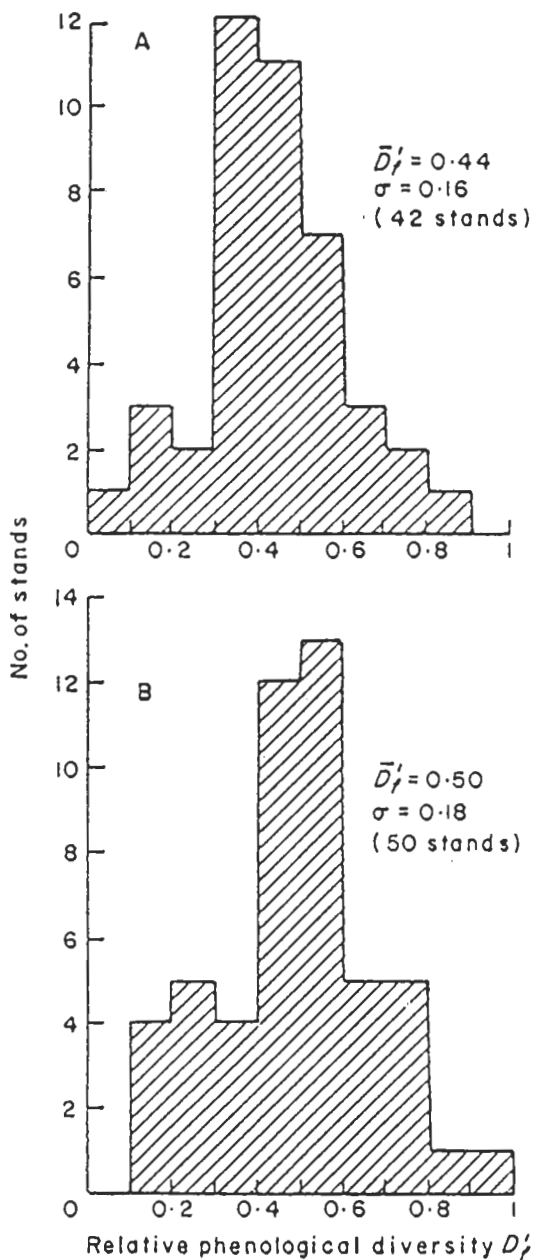
Fig. 4.2. Relative phenological diversity, per savanna stand in A a Venezuelan sample of 42 stands; B a sample of 50 stands in the western Venezuelan western llanos.
$Df = \dfrac{Df - Df\min}{Df\max - Df\min}$ $(Df = 1/\Sigma i\, pi^2)$.
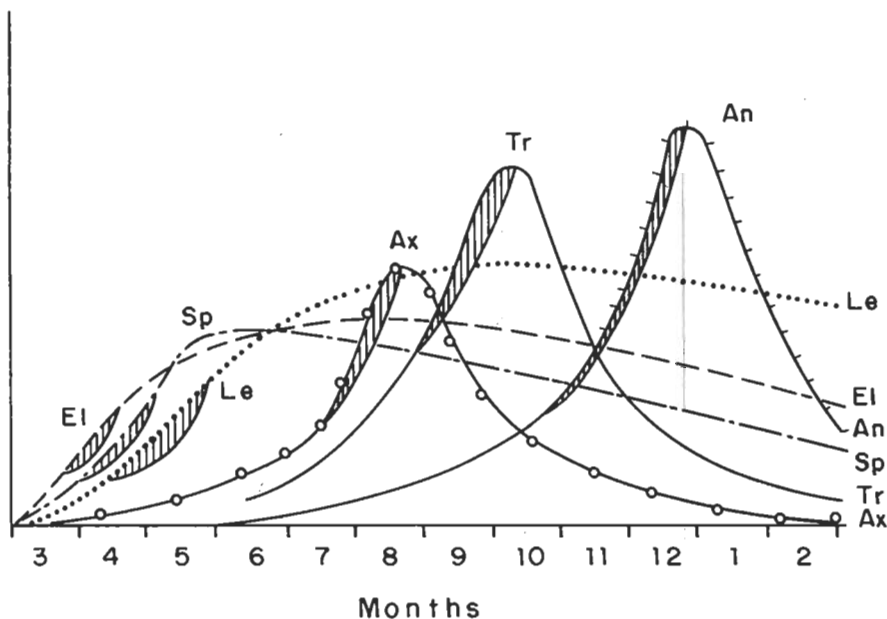(Sarmiento 1983b)

Fig. 4.3. The annual cycle of the green biomass of the six dominant grasses in the seasonal savanna in the Venezuelan llanos normally burnt in March. V*ertical hatching* indicates the flowering periods. Note the displacement of flowering and the nonoverlapping of periods of maximum groth in each species, suggesting a temporal division of the niche in the grass layer. El = *Elyonurus adustus;* Sp = *Sporobolus cubensis;* Le = *Leptocoryphium lanatum;* Ax = *Axonopus canescens;* Tr = *Trachypogon vestitus;* An = *Andropogon semiberbis.* (Sarmiento and Monasterio 1983)

others only during the dry season, whereas others grow continuously throughout the year (Monasterio and Sarmiento 1976; Lamotte 1978; Sarmiento and Monasterio 1983; Fournier 1991). Functional diversity is present within each life-form, as has been shown for evergreen trees and perennial tussock grasses (Sarmiento et al. 1985; Sarmiento 1992).
   As shown in Figs. 4.2 and 4.3, an even mixture of contrasting phenological patterns characterizes each community. Furthermore, the species also differ in demographic traits such as fecundity, seed bank dynamics, and germination (Silva and Ataroff 1985).
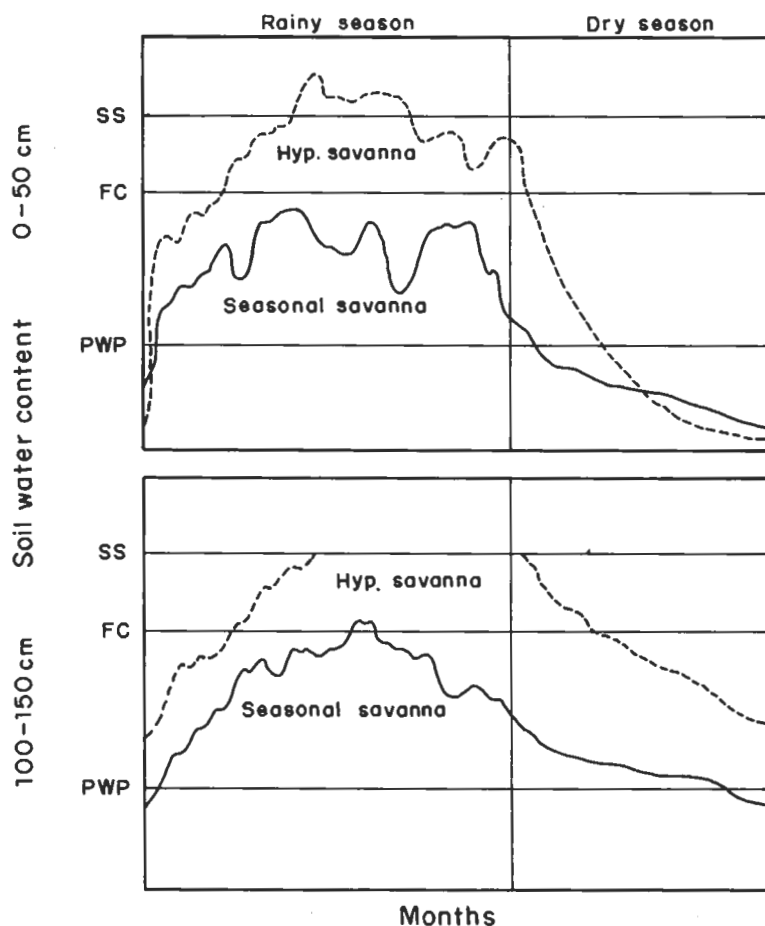
Fig. 4.4. Annual patterns of soil water content at 0-50 and at 100-150 cm in two contrasting types of tropical savannas. *SS* Soil saturation; *FC* field capacity; *PWP* permanent wilting point

4.3   Patterns of Water Availability

Plant-available moisture (PAM) is one of the crucial ecological limitations for the growth of savanna plants. PAM varies both spatially, according to depth, and temporally as a result of seasonal rainfall.

In seasonal savannas, soil water potentials are above the permanent wilting point during the rainy season, and consequently moisture is available for any plant species (Fig. 4.4). After the rainy season ends, the topsoil's water

potential drops below -1.5 MPa and it remains at values as low as -3.0 to -4.0 MPa during the dry season (San Jose and Medina 1975; Sarmiento et al. 1985; Goldstein and Sarmiento 1987; Sarmiento and Acevedo 1991). Deeper, but still within the reach of woody species, soil water potentials drop slowly, remaining higher than in the topsoil for a longer portion of the dry season (Fig. 4.4). Thus, the uppermost layers show sharper contrasts in Plant Available Moisture (PAM) from one season to the next, while deeper layers are much less seasonal. Grasses and trees certainly compete for topsoil moisture, but the deeper water is available only to deep-rooted species such as the evergreen trees.

In hyperseasonal savannas, a PAM-limited dry season alternates with a rainy season during which soil is saturated and even waterlogged. Consequently, plants experience anoxic soil conditions derived from excess of water, that induce not only functional stresses but also a high mortality of fine roots (Joly 1991).

4.4   Water Loss and the Diversity of Plant Responses

The transpiratory behavior of several species of trees and perennial grasses from various savanna regions is now well documented (Bate et al. 1982; Medina 1982; Goldstein et al. 1986, 1990; Sarmiento and Acevedo 1991). Deciduous tree species respond to water stress by shedding their foliage during the dry season. Evergreen trees, on the other hand, seem to have enough available water to cover the evaporative demands of the atmosphere throughout the year. Four evergreen trees, very characteristic of neotropical savannas – *Curatella americana*, *Byrsonima crassifolia*, *Bowdichia virgilioides* and *Casearia sylvestris* – show seasonal courses of transpiration rates more related to air VPD (Vapor Pressure Deficit) than to the alternating of dry and moist seasons (Fig. 4.5; Goldstein and Sarmiento 1987). Perennial grasses evidence a clear seasonal behavior, since they decrease their transpiration rates sharply during the rainless season (Goldstein and Sarmiento 1987).

There are important differences between the species' responses within each of these functional groups. Evergreen tree species differ in their daily patterns of stomatal conductance and transpiratory fluxes, and some of them severely restrict water losses during the midday hours (Fig. 4.6). Of the four species mentioned above, *Bowdichia virgilioides* is the most drought-avoiding species, since it shows the highest turgor-loss point, the lowest resistance to water flow, and the severest stomatal control. *Casearia sylvestris*, in contrast, is the most drought-tolerant species because it shows the lowest turgor-loss point and the most negative leaf water potential. *Curatella americana* and *Byrsonima crassifolia* seem to have intermediate drought-resistant strategies.
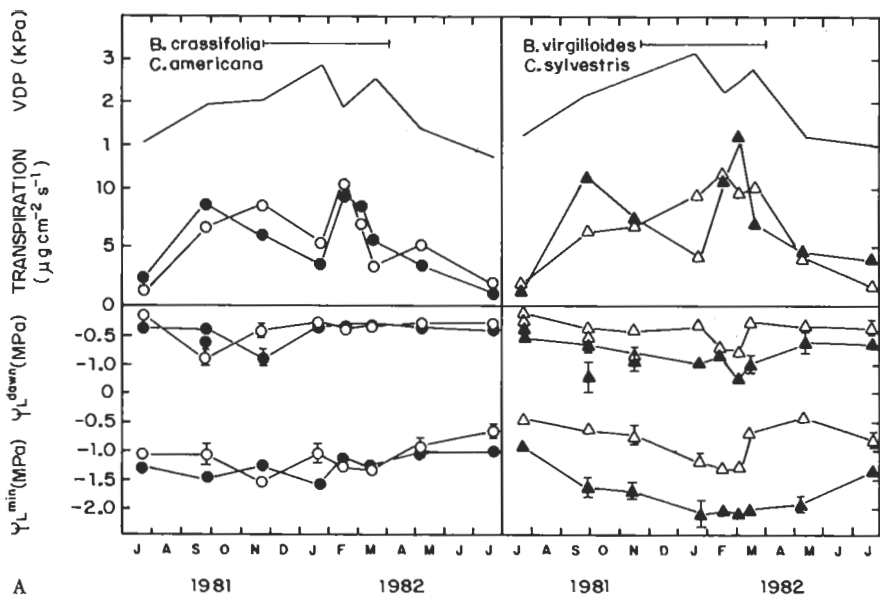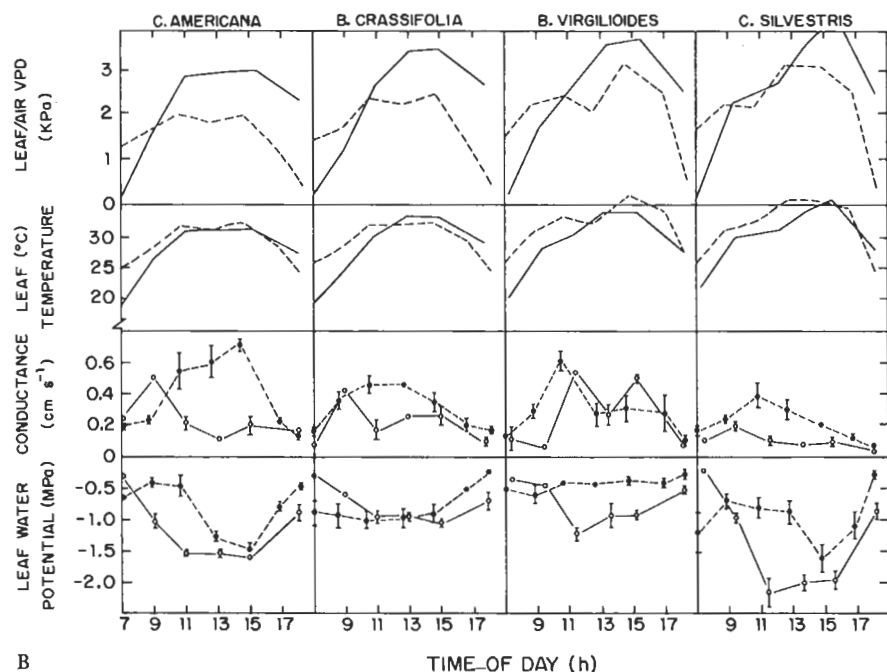
Fig. 4.5.A Annual courses of leaf-to-air vapor pressure deficit (*VPD*), transpiration, dawn leaf water potential, (ψ_L^{dawn}) and minimum leaf water potential (ψ_L^{min}) in four woody species of the Venezuelan savannas. Vertical bars represent $1 \pm$ standard error; absence of bars indicates that the standard error was smaller than the symbol. Upper segments indicate length of the dry season (Goldstein et al. 1986). B Daily courses of leaf-to-air vapor pressure deficit (VPD), leaf temperature, stomatal conductance, and leaf water potential for four woody species of the Venezuelan savannas. Dashed Lines correspond to one wet season day, the continuous line to one dry season day. (Goldstein et al. 1986)
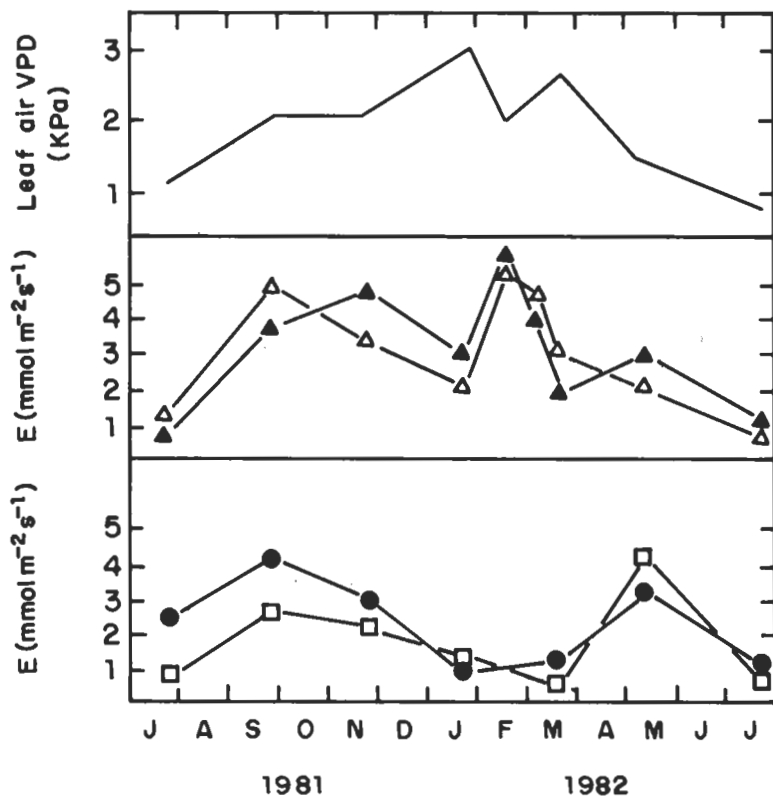
Fig.4.6. Seasonal courses of leaf-to-air vapor pressure deficit *(VDP)*, and transpiration rates *(E)* for *Curatella americana* (Δ) *Byrsonima crassifolia* (▲), *Sporobolus cubensis* (□), and *Andropogon semiberbis* (●). The first two species are evergreen trees and the last two are perennial C_4 grasses. (Goldstein et al. 1986 and unpubl. data)

Grasses also differ from each other in the minimum leaf water potential and in the actual transpiratory fluxes that they attain in the dry-season days (Goldstein and Sarmiento 1987). Concerning minimum leaf-water potential, *Sporobolus cubensis* shows a gradual decrease in values throughout the dry season, while *Trachypogon vestitus* consistently maintains lower values, and experiences a marked drop that starts in the second half of the wet season (Fig. 4.7). *Sporobolus cubensis* also exhibits a lower transpiration rate than *Andropogon semiberbis* during most of the year (Fig. 4.7). Grass species may also show contrasting behavior under water stress, when they attain low stomatal conductance. Some species, such as *Trachypogon vestitus* and *Hyparrenia rufa*, maintain assimilation rates at low conductance relatively higher than others like *Leptocoryphium lanatum* (Goldstein and Sarmiento 1987).
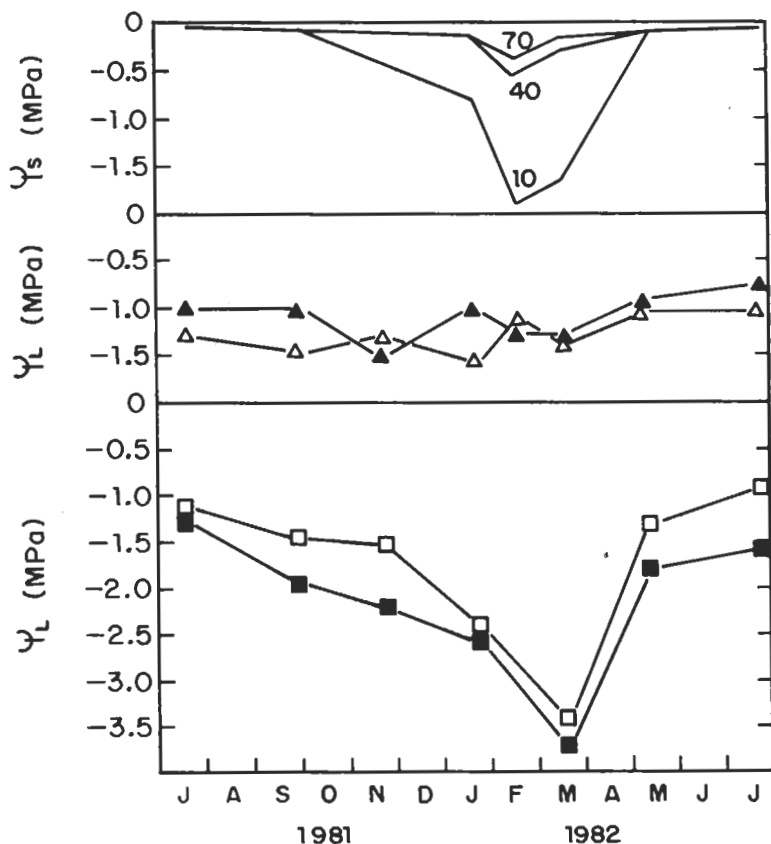
Fig.4.7. Seasonal courses of soil water potential (Ψ soil) at 10, 40, and 70 cm depth, and minimum leaf water potential (Ψ_L) for *Curatella americana* ($\triangle$), *Byrsonima crassifolia* ($\blacktriangle$), *Sporobolus cubensis* ($\square$), and *Trachypogon vestitus* ($\blacksquare$). The first two species are evergreen trees and the last two are perennial C_4 grasses. (Goldstein et al. 1986 and unpubl. data)

The pattern emerging from the diversity in grass responses is related to phenological diversity. In fact, precocious species such as *S. cubensis* and *L. lanatum*, that start regrowth and bloom immediately after the onset of the rains or even after a fire at the end of the dry season, appear to be less drought-tolerant than intermediate and late species such as *T. vestitus*, *A. semiberbis*, and *H. rufa*. Early-growing species have higher water use efficiency than lategrowers; consequently, they grow best when water is available, and they are less tolerant to adverse water conditions than late-growing species.
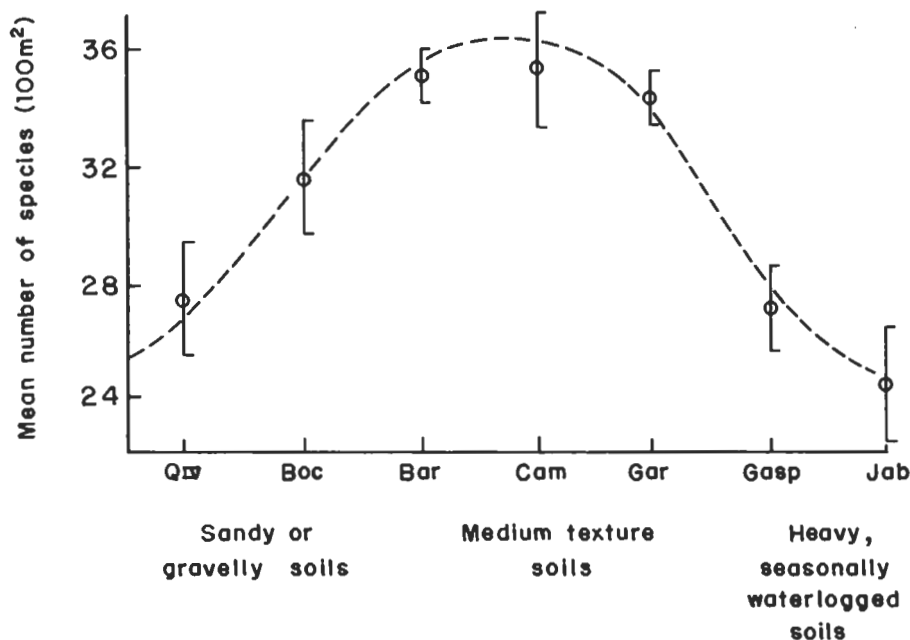
Fig. 4.8. Mean number of species of vascular plants in ten samples (100 m^2) from seven savanna communities in the Venezuelan western llanos, ordered along a soil moisture gradient. (Data from Silva and Sarmiento 1976)

4.5 Plant-Available Moisure and the Specific and Functional Diversity of Savannas

Differences in history and evolution normally tend to obscure the relationships between diversity and function in plant communities. Therefore, to avoid this, comparisons are made between communities within the same or in closely related geographical areas. Here, we will compare savanna communities from the western Venezuelan Llanos based on data from Silva and Sarmiento (1976).

Diversity, as total plant species richness, was measured along a topographic gradient (Fig. 4.8). Soil moisture and PAM vary along the gradient from well-drained soils with a long seasonal drought at one extreme, to poorly drained soils with both a long drought and a season of flooding at the other; the central part of the gradient seems to present the most favorable soil water conditions, since it is free from waterlogging and has a long PAM season. Richness is maximum under these conditions. Other measurements

of community diversity, such as richness and evenness of perennial grass species, show the same pattern of variation along the gradient. In conclusion, maximum diversity corresponds to lowest water stress

Other soil properties also change along the gradient. The dystrophic condition of the soil ameliorates from the well-drained to the poorly drained conditions. Thus, in this case, diversity responds to PAM but not PAN (Plant Available Nutrients).

Similar results were found in a more extensive study on a wide range of Venezuelan seasonal savannas (Sarmiento 1983b). Floristic diversity, measured as perennial-grass species richness, also peaks toward the more mesic conditions and decreases towards both extremes: dry sandy soils and wet, seasonally saturated soils.

Phenological diversity in the perennial grass component presents a somewhat more confused picture. Richness and evenness are higher at intermediate, neither too dry nor too wet, climatic and edaphic conditions. However, there is a tendency for each phenological group to become dominant under particular ecological conditions; precocious species on deep soils and a relatively long rainy season; early species on deep soils but a relatively short rainy season; intermediate grasses on shallow soil with a short rainy season, and late species on shallow soil with a long rainy season. The picture is far from clear, and other factors like fire and nutrients may be involved.

4.6   Conclusions

There is a hierarchy of determinants, some of them correlated to each other, that affect species composition and diversity of savanna communities. At the top of the hierarchy is the annual regime of PAM, but other determinants such as PAN, fire, and herbivory must also be considered (Solbrig 1991).

Short-term changes and period pulsation of these determinants may alter species composition and diversity. However, the functional diversity of savannas allows for only minor floristic changes. "Redundant" species within each functional group are not entirely equivalent, and hence they have different tolerances to environmental pulsation. Therefore, changing conditions may result in a certain degree of floristic replacement, without major changes in the functioning of the system. This means that savannas should be more stable in functional than in floristic terms. Only major changes in the top levels of the hierarchy of environmental determinants conceivably lead to functional changes and eventually to the complete replacement of the savanna ecosystem.

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