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9   Biodiversity and Stability in Tropical Savannas
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9.1   Introduction

The stability of savanna plant communities depends on the kind, intensity, and extent of perturbation. This chapter will discuss some aspects of the nature of perturbations taking place in savanna communities, and will put forward the hypothesis that the relative stability of a community on the face of a perturbation depends on its floristic structure. The structure of a plant community, or floristic structure, is used here in a phytosociological sense, involving not only the species composition but also the relative importance of each species. This hypothesis implies that two savanna communities exhibiting the same values of diversity (namely the same diversity index H') may differ in stability if they differ in floristic structure. The hypothesis is based on the fact that individuals from different species react differently to changes in their environment. In turn, this dissimilarity in stability will also depend on the nature of the perturbation.

Individual plant responses will affect survival and fertility at the population level. The magnitude of the connection from individual to population will depend on the species' life history traits. This is another reason why community responses to perturbations depend heavily on the floristic structure.

A perturbation can be defined as a sudden and relatively short change in the prevalent environmental conditions. Some common perturbations in savannas are changes in the prevalent climate or fire regime and in the patterns of human use (such as cattle grazing or agriculture). These disturbances have two kinds of effects: (1) those that directly modify community structure (by differential removal of individuals as in grazing or by total

replacement as in agriculture); (2) indirect effects that modify some of the prevailing physical conditions such as plant available moisture (PAM), plant available nutrients (PAN) and fire regime. As discussed above, these indirect effects may also result in variations in the structure of the community. In turn, changes in the relative importance of some species may affect the status of dependent or competing species, generating further modifications in community structure.

Stability and related properties of ecosystems are important concepts that have been formulated in different ways, using very variable terms and definitions (Harrison 1979; Connell & Sousa 1983; Holling 1986). This chapter will use stability as the property enabling a community to maintain its floristic structure on the face of an environmental perturbation. Although modeling of savanna stability has already been undertaken (Walker et al. 1981; Walker and Noy-Meir 1982), the relationships between stability and diversity are little known in tropical savannas.

9.2 Morphological and Functional Differences in Savanna Species

Different responses are expected from species differing widely in life-form, as in the case of grasses vs. savanna trees. However, species sharing the same life form, e.g., grasses, may also respond differently depending on various functional traits like photosynthetic metabolism, biomass allocation, phenology, etc. That so many grass species coexist in the same savanna is possible precisely because they differ in many traits (Sarmiento and Monasterio 1983). Coexisting savanna grasses differ in their life cycles, phenology, architecture, annual seed production, seed dormancy and germination, and photosynthetic metabolism (Sarmiento 1983a; Sarmiento and Monasterio 1983; Mott and Andrew 1985; Silva and Ataroff 1985; Silva 1987; Raventós and Silva 1988; Ernst et al. 1991; Veenendaal et al. 1993). Although the mechanisms are still to be studied, these differences result in contrasting responses to water stress, burning, shading, competition, and grazing (O'Connor 1993; O'Connor and Pickett 1992; Raventós and Silva 1988, 1995; Silva et al. 1990).

Tree species also show a wide array of morphological and functional differences, although they are not as well documented as for grasses. In neotropical savannas, tree species vary along a continuum from evergreen, sclerophyllous, and fire-resistant species at one extreme to deciduous, mesophyllous, and non-fire-resistant ones at the other. Although evergreen trees have been grouped together because they are reproductively active during the dry season (Sarmiento and Monasterio 1983), more detailed comparisons show that even closely related species differ in their

reproductive phenologies and in other aspects of their reproductive biology (Oliveira and Silva 1993). Although almost half of the Brazilian savanna (*cerrado*) tree species are dispersed by wind, there is a wide variation in dispersal syndromes and type of propagules (Oliveira and Moreira 1992).

Tree leaves vary from large, very sclerophyllous (such as in *Palicourea rigida*) to small, coriaceous leaves (such as in *Casearia sylvestris*), and these differences may be related to their responses to water stress and to nutrient stress (Goldstein and Sarmiento 1987; Sarmiento et al. 1985). Biomass allocation is also variable between tree species, particularly during the first growth stages (Moreira 1992). Trees also differ in their responses to burning (Moreira 1992).

9.3 Responses of Savanna Species to Changes in Fire Regime

9.3.1 Grass Populations

Changes in the frequency of fires can affect grass populations on two accounts: (1) direct mortality, especially of young plants; (2) increased radiation reaching the soil surface, since fire removes the dry standing matter. Savanna grasses differ in their sensitivity to these two effects. The seedlings of some species are more shade-tolerant than others, and hence these species are capable of withstanding longer periods without a fire. Some species are more resistant to burning, and hence they persist under a regime of frequent fires. In the Venezuelan savannas, seedlings and small plants of *Andropogon semiberbis* are less tolerant to the shading generated by fire exclusion than those of *Sporobolus cubensis*. On the other hand, the seedlings and young plants of *S. cubensis* are more sensitive to the effects of fire as a mortality agent than those of *A. semiberbis* (Silva et al. 1990). Populations of these species will react differently to changes in fire frequency, since both rely on seed production and germination for population growth.

Annual and perennial grass species differ in their response to changes in fire frequency. The annual grass *Andropogon brevifolius* seems able to persist under annual fire frequency equal or higher than 0.29. This is equal to a fire every third year (Canales et al. 1994). In contrast, the perennial *A. semiberbis* cannot persist under fire regimes with annual frequency below 0.83, that is exclusion of fire every sixth year (Silva et al. 1991). The perennial *Sporobolus cubensis*, which, as discussed above, is more tolerant to shade and less tolerant to fire than *A. semiberbis*, probably tolerates fire frequencies lower than 0.83. Other common grass species may also differ in their responses to fire frequency, but there is still very little published information available.

Table 9.1.A Rate of increase in tree density (N) after fire exclusion in 1961 adjusted on a yearly basis for comparison. Calculated from San José and Fariñas (1991) as N(t2) - N(t1)/ N(t1) [t2 - t1)]; "t1" and "t2" are consecutive sampling years. B Rate of increase of relative density (P) of grass species in the open grassland. Calculated from San José and Fariñas (1991) as P(t2) - P(t1)/ P(t1) x [t2 - t1]

	1969	1977	1983	1986
A				
In Open Grassland				
Curatella americana	1.14	0.15	0.78	0.14
Byrsonima crassifolia	0.45	0.11	0.14	0.004
Bowdichia virgilioides	-0.02	-0.01	0.61	0.004
Cochlospermum vitifolium		0.30	0.61	0.02
Godmania macrocarpa			16.17	0.04
Cordia hirta			3.29	-0.002
Machaerium pseudoacutifolium				0.25
In Groves				
Curatella americana	0.06	0.05	0.27	0.12
Byrsonima crassifolia	0.03	0.01	0.07	0.01
Bowdichia virgilioides	0.02	0.05	-0.01	0.01
Cochlospermum vitifolium	4.57	0.12	1.00	0.07
Godmania macrocarpa	1.86	0.09	1.21	0.09
Cordia hirta	9.00	0.27	0.27	-0.001
Machaerium pseudoacutifolium		0.25	0.94	0.22
B				
Trachypogon plumosus	-0.02	-0.06	-0.07	0.20
Axonopus canescens	0.08	0.09	-0.04	0.05
Hyparrhenia rufa		2.38	0.36	0.10

One additional source of information comes from long-term fire exclusion experiments. Data from the Biological Station in Calabozo, Venezuela (San José and Fariñas 1983, 1991) show different responses to fire exclusion from *Axonopus canescens*, *Trachypogon plumosus*, and *Hyparrhenia rufa* (Table 9.1). *Axonopus canescens* increased during the first 16 years of exclusion, whereas during the first 22 years of exclusion *T. plumosus* decreased steadily. *Hyparrhenia rufa* started to invade the area after 8 years, and increased rapidly thereafter. Changes in species presence may be due to the removal of direct mortality effects on seedlings, particularly important for seed relying species such as *A. canescens* and *H. rufa*. Also the decrease in light intensity reaching the ground seemed to have a stronger negative effect on *T. plumosus* than on the other species (San José and Fariñas 1983). Since we already know that *T. plumosus* is a strong competitor (Raventós and Silva 1995), it is probable that its decrease is favoring the increase of the other species. After prolonged fire exclusion, shifts in population growth occur, as shown in Table 9.1. Additional factors operating in this case may be rainfall, soil, and nutrient status.

The importance of the species composition for savanna stability is reinforced by a very transient seed bank in the soil, since seeds germinate readily and have limited survival in the field (Silva and Ataroff 1985; O'Connor and Pickett 1992). The seeds produced by precocious and early flowering grasses germinate as soon as they reach wet ground. The seeds produced by intermediate and late flowering species stay dormant on the surface of the soil throughout the year and will germinate at the beginning of the following rainy season. The seeds of tree species probably germinate during the first weeks of the wet season, although there are no detailed studies on the dynamics of tree seed banks in the field. Seeds that do not germinate do not survive and there is no apparent permanent seed bank in the savanna soil. Consequently, seedling recruitment depends on current seed production, and this in turn depends on the size of the population, the fraction of individuals blooming and their productive performance in that particular year. Further studies are needed to provide information on these aspects.

9.3.2   Tree Populations

Tree density increases in response to a decrease in fire frequency as has been shown in several exclusion experiments (Menaut 1977; San José and Fariñas 1983; Coutinho 1990). Furthermore, new tree species invade the savanna during fire exclusion, increasing the diversity of the tree layer. However, the various tree populations react differently to the change in fire regime, and therefore the savanna response to this perturbation depends on the initial composition of the tree layer. Propagule availability from neighboring forests is also important.

In the Calabozo's exclusion experiment mentioned above, San José and Fariñas (1991) recorded differences in population growth between and within sclerophyllous-evergreen and mesophyllous-deciduous tree species (Table 9.1). In the open savanna, evergreen trees increased rapidly in numbers after exclusion, whereas deciduous trees exhibited a long lag phase of at least 16 years. In the groves, in contrast, the deciduous trees increased strikingly during the first 8 years after exclusion, whereas the evergreen trees changed little. Among the sclerophyllous trees, *Curatella americana* showed a high growth rate compared to *Bowdichia virgilioides* (Table 9.1). Among the deciduous trees, *Cochlospermum vitifolium* needed only 8 years of exclusion to start increasing in the open grassland, whereas all the other deciduous species needed much longer.

These results are not easy to interpret based only on the effects of fire exclusion. Deciduous trees are little resistant to fire, especially in the early growth stages; therefore they are unable to invade the frequently burnt grassland, and are restricted to small groves protected from burning. After exclusion of fire, these populations are expected to rapidly colonize the

grassland. However, fast-growing trees with wind-dispersed seeds such as *Cochlospermum vitifolium* and especially *Godmania macrocarp*a, increased very slowly in the fire-free grassland. In the 1983 census (22 years of exclusion), both species showed a burst of increase, especially *G. macrocarpa,* which during the 6 years between 1977 and 1983 increased 98 times in number (from 6 to 588 stems; San José and Fariñas 1991).

One plausible explanation for this lag is that in the period 1977-1983 other disturbances took place and acted synergically with the lack of fire to promote or restrict tree populations' growth. Alternatively, some changes in the nutrient status of the soil may be needed in the open grassland but not in the groves, for the trees to become established. In this regard, Fölster (1986) suggested that nutrient impoverishment by recurrent fires following deforestation and establishment of the grassland is the main cause deterring the recovery of the forest in the Gran Sabana (southern Venezuela). However, groves and open grasslands from the Orinoco Llanos do not seem to be significantly different in soil nutrient status (Sarmiento 1984). In any case, the Calabozo exclusion experiment shows that all tree species reacted positively to fire exclusion, but differ in the speed and magnitude of their reactions (San José & Fariñas 1991).

9.4   Responses to Changes in PAM Regime

The seasonal pattern in plant-available moisture (PAM) is determined by the rainfall regime. In turn, soil characteristics (topographic position, structure, and texture) influence water availability throughout the year; however, they change on a geomorphologic time scale, except when erosive processes are accelerated by land use. Consequently, short-term perturbations in PAM regime do not originate in the soil but rather result from changes in rainfall. These short-term changes seem to be common, although there is little published information on climate trends in savannas to document it. In southern Africa, pulses in rainfall are responsible for changes in the size of populations and the structure of savanna communities on different soils and are considered an overriding factor in several studies on the effects of grazing and fire (O'Connor 1985). A conclusion from the O'Connor analysis of southern Africa experiments is that drought spells induce important changes in savanna composition, and these effects increase with aridity. On the other hand, savanna resilience to drought (resilience defined as the ability of the system to return to the previous condition after a disturbance, Harrison 1979) seems to be high. Another important conclusion in O'Connor (1985) is the influence of tree density on the changes in the grass layer. When the woody/grass ratio (density of trees) was stable, the grassland component was not affected by overgrazing.

However, when changes in tree density took place during the experiment, the grass layer was very sensitive to grazing and overgrazing, especially during critical drought years. This implies a positive feedback for the whole system, since stability of one component (trees) results in added stability of another component (grasses). Unfortunately, these are very preliminary conclusions, and to my knowledge there are no published studies relating rainfall variations with savanna structural changes.

Several studies enforce the conclusion that savanna community is primarily responding to PAM regime (Medina and Silva 1990; Solbrig 1990; Teague and Smit 1992). Some results emphasize the differences in plant response to water stress in grasses and trees from seasonal savannas (see Chap. 6). Savanna grasses are tolerant to negative leaf water potentials. However, they differ in the degree of tolerance to water stress (Goldstein and Sarmiento 1987). Furthermore, grass species are distributed differentially along humidity gradients reflecting differences in their responses to the length of the dry season and to water logging (Silva and Sarmiento 1976a,b). These preferences are seemingly related to the phenological behavior of the population. Sarmiento (1983b) suggested that change in the length of the dry season results in increased representation of some phenological groups at the expense of other groups. Although Sarmiento's study was not conclusive, it provides support for this hypothesis. He concluded that early onset of rains would favor species blooming very early in the wet season ('precocious species'), whereas a prolonged rainy season would favor species blooming at the end of the wet season („late species"); a shortening of the rainy season was detrimental to both types but favorable to species blooming in the middle of the wet season („early" and „intermediate" species).

Trees are probably more sensitive than grasses to changes in water availability. Wet spells seem to be responsible for an increase in tree density in the dryer savannas of southern Africa (O'Connor 1985). Quaternary fluctuations in annual rainfall are related to major changes in tree densities in savannas and in the forest-savanna boundaries in South America (van der Hammen 1974, 1983) and Madagascar (Burney 1993). To what extent the response of the woody component to changes in water availability throughout the year depends on the species composition is not known. Evergreen trees with high underground biomass and large leaves (e.g., *Curatella americana*) depend on continuous water supply from the subsoil. Extended dry seasons for several consecutive years will have a negative effect on the growth of these trees due to progressive depletion of subsoil water. Goldstein and Sarmiento (1987) suggested that under these conditions, deciduous trees or trees with smaller leaf size and higher tolerance to drought should be favored.
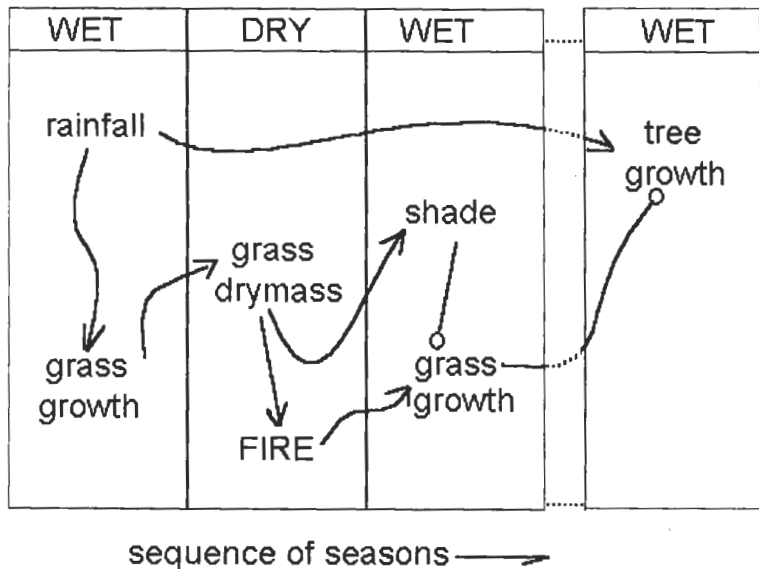
Fig. 9.1. Diagram showing possible interactions between savanna determinants (rainfall, fire) and savanna components (grass biomass and tree biomass) throughout a sequence of seasons. An *arrow* indicates positive effect; a *circle* means negative effect (see text for explanation)

Perturbations are not totally independent. On the contrary, there are strong interactions among rainfall, biomass, fire frequency and intensity, grazing, and nutrient fluxes in seasonal savannas. A pulse of increased annual rainfall will increase grass biomass during that season, and this will result in an increase in the amount of standing dead biomass during the next dry season. As a consequence, the probabilities of burning also increase. Alternatively, if there is no fire, shading will increase during the following wet season, reducing grass growth (Fig. 9.1). The consequences of a higher rainfall pulse may not be restricted to the short term. Tree growth and recruitment will increase, especially if fire does not occur. This will alter the tree/grass ratio in following years, affecting grass growth and reproduction and influencing fire and grazing regimes.

9.5   Conclusions

Savanna plants differ widely in their responses to changes in fire and humidity regime. The direction and extent of the changes the savanna community undergoes as a consequence of environmental perturbations

depends on what species are facing the perturbation. These "initial conditions" in savanna community structure may be more important than species richness or other diversity index, and have to be considered to study the dynamics of savannas as nonlinear systems (Nicolis 1992). The importance of the species composition for savanna stability is reinforced by the transient seed bank in the soil. Although it has been claimed that functional stability of experimental grasslands perturbed by a drought spell depended on species richness per se (Tilman and Downing 1994), the response in this case was clearly tied to the presence of particular, drought-resistant species in the richer communities.

The diversity of savanna plant responses to environmental perturbations may explain the persistence of savanna communities within a broad range of environmental variation. Current knowledge suggests that savanna persists under the control of seasonal climate, fluctuating within certain bounds as the result of the occurrence of climatic disturbances and its concatenated effects on fire, grazing, and other factors.

Savanna studies have emphasized the similarities among species and classified them into functional groups, such as evergreen-sclerophyllous trees or perennial bunch grasses. To better understand savanna responses to perturbation, it is convenient to shift the focus to the comparative analysis of species morphology and their functional differences. The initial hypothesis of this chapter can be used to further research on the role these differences are playing in the stability of savanna communities.

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