Published in: Solbrig, O.T., Medina, E. & Silva, J.F. (Editors). *Biodiversity and savanna ecosystem processes: a global perspective.* Springer-Verlag, Berlin. 233 pp. 1996.

9 Biodiversity and Stability in Tropical Savannas

Juan F. Silva.
Centro de Investigaciones Ecológicas de los Andes Tropicales (CIELAT). Facultad de Ciencias. ULA. Mérida, Venezuela.-

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, agriculture, etc.). 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 (Connel & Sousa 1983; Harrison 1979; 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 & 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 & Monasterio 1983). Coexisting savanna grasses differ in their life cycles, phenology, architecture, annual seed production, seed dormancy and germination, and photosynthetic metabolism (Ernst et al., 1991; Mott & Andrew 1985; Raventós & Silva 1988; Sarmiento 1983a; Sarmiento & Monasterio 1983; Silva 1987; Silva & Ataroff 1985; 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 & Pickett 1992; Raventós & Silva 1988, 1994; 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 as reproductively active during the dry season (Sarmiento & 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 & 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 & Moreira 1992).

Tree leaves vary from large very sclerophyllous (like in *Palicourea rigida*) to small coriaceous leaves(like in *Casearia sylvestris*) and these differences may be related to their responses to water stress and to nutrient stress (Goldstein & 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.

One additional source of information comes from long-term fire exclusion experiments. Data from the Biological Station in Calabozo, Venezuela (San José & Fariñas 1983, 1991) show different responses to fire exclusion from *Axonopus canescens, Trachypogon plumosus* and *Hyparrenia rufa* (Table 1). *Axonopus canescens* increased during the first 16 years of exclusion, whereas during the first 22 years of exclusion *T. plumosus* decreased steadily. *Hyparrenia 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 & Fariñas 1983). Since we already know that *T. plumosus* is a strong competitor (Raventós and Silva 1994), 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 1. Additional factors operating in this case may be rainfall, and soil nutrient status.

9.3.2. Tree populations

Tree density increases in response to a decrease in fire frequency as has been shown in several exclusion experiments (San José & Fariñas 1983; Coutinho 1990; Menaut 1977). 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 & 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 sixteen 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.

TABLE I

A.- Average annual relative increase in tree density after
fire exclusion in 1961. (Calculated from San José & Fariñas, 1991)
Relative annual rate of increase= N(t) - N(t-1)/ N(t) x [t - (t-1)]

	year			
	1969	1977	1983	1986
IN GRASSLAND:				
Curatella	1.1429	0.1464	0.7835	0.1434
Byrsonima	0.4472	0.1132	0.1427	0.0040
Bowdichia	-0.0186	-0.0125	0.6111	0.0040
Cochlospermum		0.3038	0.6181	0.0209
Godmania			16.1667	0.0357
Cordia hirta			3.2857	-0.0015
Machaerium				0.2523
IN GROVES:				
Curatella	0.0557	0.0504	0.2719	0.1235
Byrsonima	0.0309	0.0065	0.0728	0.0098
Bowdichia	0.0204	0.0469	-0.0091	0.0128
Cochlospermum	4.5714	0.1174	0.9974	0.0701
Godmania	1.8571	0.0893	1.2083	0.0892
Cordia hirta	9.0000	0.2695	0.2715	-0.0013
Machaerium		0.2500	0.9444	0.2167

B. Average annual rate of increase of grass species presence
in the open grassland (calculated from San José & Fariñas, 1991).
Relative annual rate of increase= P(t) - P(t-1)/ P(t) x [t - (t-1)]

Trachypogon	-0.0204	-0.0634	-0.0718	0.1982
Axonopus	0.0779	0.0938	-0.0434	0.0492
Hyparrenia		2.3750	0.3583	0.0952

These results are not easy to interpret based only on the effects of fire exclusion. Deciduous trees are weakly resistant to fire, especially in the early 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 *macrocarpa* 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* that during the six years between 1977 and 1983 increased 98 times in number (from 6 to 588 stems; San José & Fariñas 1991).

One plausible explanation for this lag is that in the period 1977-83 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 grassland 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 are reacting positively to fire exclusion, but they 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 soil and are considered an overriding factor in several studies on the effects of grazing and fire (O'Connor 1985). A conclusion from 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 throughout 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 in 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 & Silva 1991; Solbrig 1990; Teague & Smit 1992). Some results emphasize the differences in plant response to water stress in grasses and trees from seasonal savannas (see Chapter 6 in this book). Savanna grasses are tolerant to negative leaf water potentials. However, they differ in the degree of tolerance to water stress (Goldstein & 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 waterlogging (Silva & Sarmiento 1976a, 1976b). These preferences are seemingly related to the phenological behavior of the population. Sarmiento (1893b) 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 fluctuactions 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 & Sarmiento (1987) suggested that under these conditions, deciduous trees or trees with smaller leaf size and higher tolerance to drought should be favored.

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 (Figure 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.

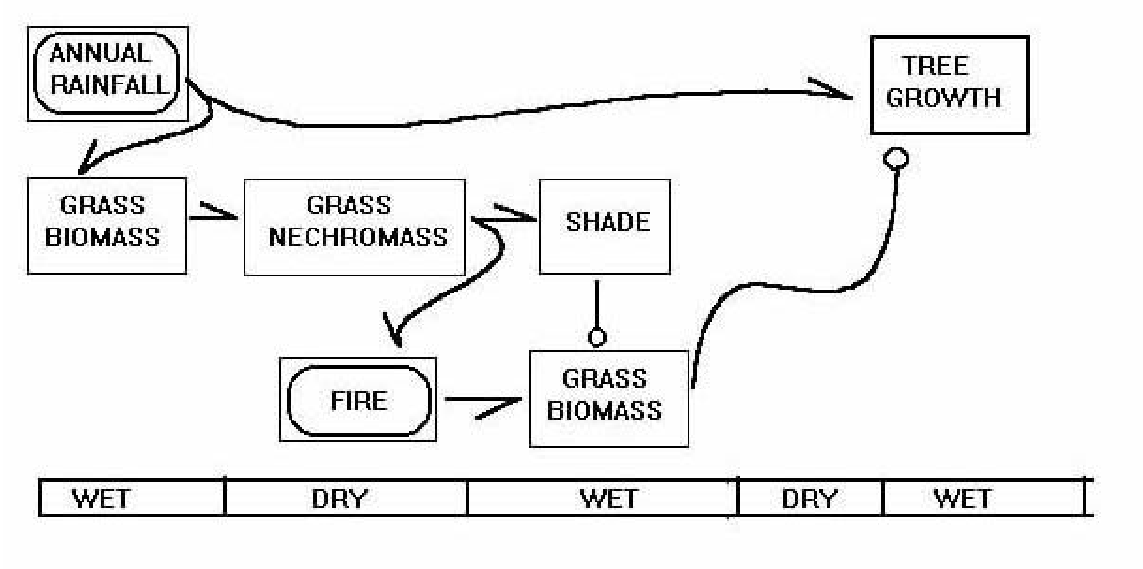

Figure 9.1. Diagram showing possible interactions between savanna determinants (rainfall, fire) and savanna components (grass biomass and tree biomass) throughout a sequence of seasons. An arrow indicates positive effect; a circle means negative effect (see text for explanation).

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). Although it has been claimed that functional stability of experimental grasslands perturbed by a drought spell depended on species richness per se (Tilman & Downing 1994), the response in this case was clearly tied to the presence of particular, drought resistant species in the richer communities.

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 (O’Connor & Pickett 1992; Silva & Ataroff 1985). 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 is depending 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.

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 classify then 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 morphological and functional differences. The initial hypothesis of this paper can be used to further research on the role these differences are playing in the stability of savanna communities.

Acknowledgments

I thank Guillermo Sarmiento and Aura Azócar for suggestions on an earlier draft of this manuscript. I am also very grateful to Otto T. Solbrig for valuable criticism and suggestions. This research is being partially funded by CDCHT-ULA grant C-344-90.

References

Burney DA (1993) Late Holocene changes in Madagascar. Quaternary Research (Orlando) 40:98-106

Canales MJ, Silva JF, Caswell H, Trevisan MC (1994) A demographic study of an annual savanna grass (*Andropogon brevifolius* Schwarz) in burnt and unburnt savanna. Acta Oecologica, in press.

Coutinho LM (1990) Fire in the ecology of the Brazilian cerrado. In: Fire in the Tropical Biota. (Ed: Goldammer,JG) Springer-Verlag, Berlin, pp.82-105.

Ernst WHO, Kuiters AT, Tolsma DJ (1991) Dormancy of annual and perennial grasses from a savanna of southeastern Botswana. Acta Oecologica 12:727-739.

Fölster H (1986) Forest-savanna dynamics and desertification process in the Gran Sabana. Interciencia 11(6), 311-316.

Goldstein,G; Sarmiento,G (1987): Water relations of trees and grasses and their consequences for the structure of savanna vegetation. In: Determinants of Tropical Savannas. (Ed: Walker,BH) IRL Press, Oxford, pp.13-38.

Hammen T van der (1983) The palaecology and palaeogrography of savannas. In: Bourliere F (ed), Tropical Savannas. Elsevier, Amsterdam. pp. ?

Harrison GW (1979) Stability under environmental stress: resistance, resilience, persistence, and variability. American Naturalist 113: 659-669.

Holling CS (1986) The resilience of terrestrial ecosystems: local surprise and global change. In: Clark WC & Munn RE (Editors), Sustainable Development of the Biosphere. Cambridge Univ. Press, pp. 292-317.

Medina E, Silva JF (1990) The savannas of northern South America: a steady state regulated by water-fire interactions on a background of low nutrient availability. Journal of Biogeography 17:403-413.

Menaut JC (1977) Evolution of plots protected from fire for 13 years in a Guinea Savanna of Ivory Coast. Actas IV Simposium Internacional de Ecología Tropical, pp. 540-558. Impresora de la Nación, Panamá.

Moreira AG (1992) Fire protection and vegetation dynamics in the Brazilian Cerrado. Ph.D. Dissertation, Harvard University.

Mott,JJ; Andrew,MH (1985): The effect of fire on the population dynamics of native grasses in tropical savannas of north-west Australia. Proc. Ecol. Soc. Aust 13, 231-239.

Nicolis G (1992) Dynamical systems, biological complexity and global change. In Solbrig OT, van Emdem HM, van Oordt PGWJ, Biodiversity and Global Change. IUBS Paris, 21-32.

O'Connor TGO (1985) A synthesis of field experiments concerning the grass layer in the savanna regions of southern Africa. SANSP # 114. Foundation for Research Development. Pretoria.

O'Connor TGO (1993) The influence of rainfall and grazing on the demography of some African savanna grasses: A matrix modelling approach. Journal of Applied Ecology 30:119-132.

O'Connor TGO, Pickett GA (1992) The influence of grazing on seed production and seed banks of some African savanna grasslands. Journal of Applied Ecology 29:247-260

Oliveira PE, Silva JCS (1993) Reproductive biology of two species of Kielmeyera (Guttiferae) in the cerrados of central Brazil. Journal of Tropical Ecology 9:67-79.

Oliveira PE, Moreira AG (1992) Anemocoria em espécies de cerrado e mata de galeria de Brasilia, DF. Revista Brasileira de Botánica 15: 163-174.

Raventós,J; Silva,JF (1988): Architecture, seasonal growth and interference in three grass species with different flowering phenologies in a tropical savanna. Vegetatio 75, 115-123.

Raventós J, Silva JF (1994) Competition effects and responses to variable number of neighbors in two tropical savanna grasses. Journal of Tropical Ecology 10: (in press).

San José JJ, Fariñas MR (1983) Changes in tree density and species composition in a protected *Trachypogon* savanna, Venezuela. Ecology 64:447-453.

San José JJ, Fariñas MR (1991) Temporal changes in the structure of a *Trachypogon* savanna protected for 25 years. Acta Oecologica 12: 237-247.

Sarmiento G (1983a) The savannas of tropical America. In Bourlière,F (ed), Tropical Savannas. Elsevier, Amsterdam, 245-288.

Sarmiento G (1983b) Patterns of specific and phenological diversity in the grass community of the venezuelan tropical savannas. Journal of Biogeography 10: 373-391.

Sarmiento G (1984) The Ecology of Neotropical Savannas. Harvard University Press, Cambridge, MA. USA. 235 pages.

Sarmiento G & Monasterio M (1983) Life forms and phenology. In: Bourliere F. (Editor), The Tropical Savannas. Elsevier, Amsterdam, pp. 79-108.

Sarmiento G , Goldstein G & Meinzer F (1985) Adaptive strategies of woody species in neotropical savannas. Biological Review 60:315-355

Silva JF (1987) Responses of savannas to stress and disturbance: species dynamics. In: Walker, B.H. (Editor), Determinants of tropical savannas. IRL Press, Oxford, UK pp. 141-156.

Silva JF, Sarmiento G (1976a) La composición de las sabanas de Barinas en relación con las unidades edáficas. Acta Científica Venezolana 27:68-78.

Silva JF, Sarmiento G (1976b) Influencia de factores edáficos en la diferenciación de las sabanas. Análisis de componentes principales y su interpretación. Acta Científica Venezolana 27:141-147.

Silva JF, Ataroff M (1985): Phenology, seed crop and germination of coexisting grass species from a tropical savanna in western Venezuela. Acta Oecologica, Oecologia Plantarum 6, 41-51.

Silva JF, Raventós J, Caswell H (1990) Fire, fire exclusion and seasonal effects on the growth and survival of two savanna grasses. Acta Oecologica. 11: 783-800.

Silva JF, Raventós J, Caswell H, Trevisan MC (1991) Population responses to fire in a tropical savanna grass: a matrix model approach. Journal of Ecology 79:345-356.

Solbrig OT (editor) (1990) Savanna modelling for global change. Biology International, special issue # 24.

Teague WR, Smit GN (1992) Relations between woody and herbaceous components and the effects of bush clearing in southern African savannas. Journal of Grassland Society of South Africa 9:60-71.

Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. Nature 367: 363-364.

Hammen T van der (1974) The pleistocene changes of vegetation and climate in tropical South America. Journal of Biogeography 1:3-26.

Veenendaal EM, Shushu DD, Scurlock JMO (1993) Responses to shading of seedlings of savanna grasses (with different C4 photosynthetic pathways) in Botswana. Journal of Tropical Ecology 9:213-229.

Walker BH, Noy-Meir I (1982) Aspects of the stability and resilience of savanna ecosystems. In: Huntley BJ & Walker BH (eds) Ecology of Tropical Savannas. Springer-Verlag. Berlin.

Walker BH, Ludwig D, Hooling CS, Peterman RM (1981) Stability of semiarid savanna grazing systems. Journal of Ecology 69:473-498.