FUNCTIONAL ROLES OF BIODIVERSITY

A Global Perspective

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8 Biodiversity and Tropical Savanna Properties: A Global View[1]

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8.1 INTRODUCTION

Savannas are the most common vegetation type in the tropics and subtropics. Broadly defined as ecosystems formed by a continuous layer of graminoids (grasses and sedges) and a discontinuous layer of trees and/or shrubs of variable extent, savannas are found over a wide range of rainfall, temperature and soil conditions. The one constant climatic characteristic of tropical savannas is rainfall seasonality. Yet the duration of the dry season can vary from three to nine months, with a mode of five to seven months.

Almost one-fifth of the world's population lives in areas that are at present, or were recently, covered with savanna vegetation (Young and Solbrig 1993; Solbrig 1994), many of them in rural societies that depend on herding or subsistence agriculture. Per capita food production in these communities is usually low, the result of a variety of environmental, social and economic constraints. Because rainfall in these regions is highly seasonal and variable, primary production is uneven and unpredictable in space and time, particularly in low-rainfall areas. Many savanna soils are nutrient-poor, particularly in high-rainfall areas, which is reflected in low crop yields and the poor nutritional quality of natural pastures. Compounding the effects of these factors is the dual nature of land use in many savanna areas: the most productive lands are set aside for cash crops, while the poorer lands are used for local food production or extensive cattle grazing (Kowal and Kassam 1978; Klink *et al.* 1993; Lane and Scoones 1993). Combined with the rapid growth of human populations in the tropics, this pattern of use is bringing about a rapid transformation of savanna landscapes, resulting in many cases in degraded environments, reduced productivity, low carrying capacity and loss of species.

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[1]An extensive report on this subject can be found in Solbrig, O.T., Medina, E. and Silva, J. (1996) *Biodiversity and Savanna Ecosystem Processes: A Global Perspective*. Springer, Berlin, in press.

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Tropical savannas have high species diversity, especially when compared with temperate grasslands and dry tropical woodlands. So, for example, 2366 species of phanerogams (Filgueiras and Pereira 1994) grow in the savannas of the small area of the Federal District of Brasilia. It has been estimated that the entire cerrado has over 10 000 vascular plant species (Ratter, personal communication 1995), while there are fewer than 6000 species in the pampas of Argentina, Uruguay and southern Brazil (Cabrera 1968; Rosengurtt *et al.* 1970), an area of similar size. However, there is still no complete inventory of the biota of any tropical savanna. Best known are vascular plants, birds and mammals; least known are invertebrates, especially non-arthropods, fungi and protists.

Savannas from different continents share very few Linnaean species, particularly among the woody elements. The invasion of American and Australian savannas by African grasses is a recent phenomenon of human origin. Within an area, however, different savanna types often share common species (Sarmiento 1984, 1994; Medina and Huber 1992). Savanna species are usually more closely related to species in other local vegetation types than to savanna species in other continents. So, for example, the phylogenetic affinities of the woody flora of the Brazilian savannas, known as *cerrado*, are with the Amazonian flora rather than with the flora of west Africa; physiognomically, however, the cerrado is more similar to the savannas of West Africa than to the Amazonian forest. In turn, African savanna species, as is also true for non-savanna ecosystems, are phylogenetically more related among themselves and with species from the wet forest than they are with savanna vegetation in other continents. African savannas (Menaut 1983) are almost as rich in species as the African rain forests, and Australian savannas have more species than neighboring wet forests.

The physiognomic similarity of tropical savannas in different regions of the world is supposedly the result of convergent evolution, predicated primarily on the basis of the vascular vegetation, especially the presence of a continuous layer of grasses. However, the Gramineae are a very stereotyped family of angiosperms, i.e. all grasses have the same basic architecture, and therefore the characteristics of savanna grass species cannot necessarily be attributed to convergence evolution. It is more likely that savannas result from parallel evolution from common ancestors under more or less similar circumstances, rather than from dissimilar ancestors. It is likely that the differences between savanna grasses are as great as the similarities (Eiten 1972), but no rigorous studies have been conducted.

Tropical savannas are very heterogeneous systems at all scales of analysis, from the individual patch to the regional level (Solbrig 1991a). This heterogeneity makes it difficult to define tropical savannas with precision and inclusiveness, and no general consensus has emerged among researchers regarding what is to be considered a tropical savanna. Broadly defined,

Table 8.1 Physiognomic types of savanna (according to Sarmiento 1984)

1. Savannas without woody species taller than the herbaceous stratum: *Grass savannas or grasslands*

2. Savannas with low (less than 8 m) woody species forming a more or less open stratum
    (a) Shrubs and/or trees isolated or in groups; total cover of woody species less than 2%: *Tree and shrub savanna*
    (b) Total tree/shrub cover between 2% and 15%: *Savanna woodland, wooded grassland, or bush savanna*
    (c) Tree cover greater than 15%: *Woodland*

3. Savannas with trees over 8 m
    (a) Isolated trees with less than 2% cover: *Tall-tree savanna*
    (b) Tree cover 2–15%: *Tall savanna woodland*
    (c) Tree cover 15–30%: *Tall wooded grassland*
    (d) Tree cover above 30%: *Tall woodland*

4. Savannas with tall trees in small groups: *Park savanna*

5. Mosaic of savanna units and forests: *Park*

savannas can be subdivided into a number of regional types (Table 8.1; Sarmiento 1984, 1992) based on rainfall seasonality characteristics and density of woody vegetation. A first distinction is between dry (roughly less than 700 mm) and moist (more than 700 mm rainfall) savannas. Within the moist savannas, we can distinguish seasonal savannas, where a period of positive moisture balance alternates with a negative one; semi-seasonal savannas, which suffer a long period of water surplus, and hyperseasonal savannas, where plants suffer a period of water deficit during the dry season and one of water surplus during the wet season. Seasonal wet savannas prevail in America; both wet and dry savannas are found in Africa, and in Australia dry savannas predominate. Natural and anthropogenically induced changes in climate, in nutrients, in fire regime and in herbivory can displace the borders of the areas occupied by different types of savanna vegetation, as well as the borders with other types of vegetation: humid forests and semi-deserts. A good example is provided by the border between the Brazilian cerrado and the tropical forest. It is well documented (Van der Hammen 1983; Furley *et al.* 1992) that during the Pleistocene dramatic expansions and shrinkages took place in the extent of the cerrado.

Savannas are also very heterogeneous at a more restricted scale. Small gallery forests with entirely different floristic elements along streams and moist areas grow within a sea of graminoid-dominated savanna vegetation. In turn, wooded savannas are dotted with small islands of woodlands from which grasses are essentially absent, and with strips of pure grassland
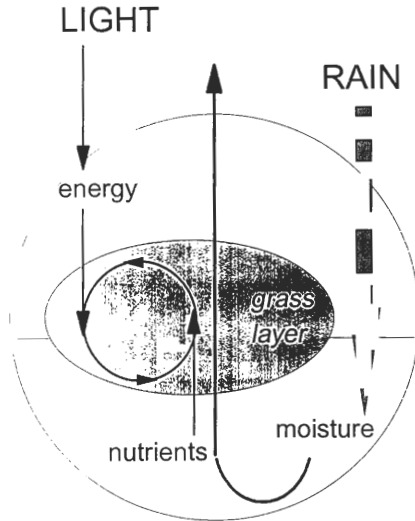
Figure 8.1   Diagram showing the coupling of nutrient and energy flows to the water flow through the grass layer of the savanna ecosystem. Pulses of rain, on a seasonal basis or within the wet season, determine the inflow of energy and materials

without or with very few trees and shrubs (Figure 8.1). Moisture, geomorphological factors, fire and herbivory are the principal determinants of this heterogeneity. So for example in the savannas of the Orinoco, the density of the woody vegetation varies with soil depth and with the age of the deposits (Silva and Sarmiento 1976a,b). This heterogeneity raises the question whether savannas should be considered as a single ecosystem, or whether they represent a diversity of ecosystems with poorly defined borders.

Most savanna syntheses have emphasized the similarities in structure and function rather than the differences in savanna ecosystems (Bourliere 1983; Sarmiento 1984; Tothill and Mott 1985). One such approach was the RSSD (Responses of Savannas to Stress and Disturbance) program of the Decade of the Tropics, sponsored by IUBS, that developed a set of hypotheses that predict the function of tropical savannas (Frost *et al*. 1986; Walker 1987; Sarmiento 1990; Werner 1991; Young and Solbrig 1993). The RSSD postulated four principal selective forces – which were called determinants – to explain some of the common features and differences in savanna structure and function. These are: (1) plant-available moisture (PAM); (2) plant-available nutrients (PAN); (3) fire; (4) herbivory. These determinants interact at all ecological scales from landscapes to local patches, but their relative importance differs with scale (Medina and Silva 1990; Solbrig 1991a).

According to the RSSD model, PAM and PAN are the principal determi-

nants of savanna structure at the higher scales. They circumscribe what was called the PAM–AN plane. Where PAM has high values mesic woody elements dominate, and as PAM increases the savanna eventually gives way to a moist forest. When PAM has very low values drought-adapted species become more numerous, and if the values of the PAM–AN plane get very low the savanna is replaced by a semi-desert. Between these two extremes the gamut of savanna types is encountered. To a limited extent PAM- and PAN compensate each other: low humidity regimes with relatively high nutrient levels, such as the Serengeti in Kenya, have a savanna-grassland and not a semi-desert vegetation; likewise areas with high rainfall but low nutrients, such as the American Llanos del Orinoco and the west African Guinea savannas in the Lamto area, have a savanna rather than a forest vegetation. Within savanna ecosystems, the local effects of the patchy distribution of soil types and topographic features modify PAM and PAN, and together with fire and herbivory determine the density of the tree layer, the productivity of the system, and the rates of nutrient and water flow through the system (Frost *et al.* 1986). Yet PAM and PAN are general determinants of vegetation, and their power in predicting some savanna properties cannot be considered sufficient evidence for the uniqueness of the savanna ecosystem.

In this chapter we address the following null hypothesis: "Removal and additions of species that produce changes in spatial configuration of landscape elements will have no significant effect on ecosystem functional properties of savannas over a range of time and space scales" (Solbrig 1991b). Addition or removal of species from an ecosystem will change both the species richness and its evenness, (Pielou 1975),and it is important that both these aspects be considered. Furthermore, the effect of the addition or removal of species will depend on the morphological, physiological, demographic and trophic characteristics of the species. Clearly the effect will not be the same if the dominant tree is removed from a savanna, or if a rare leaf-mining insect is removed. While there are well-established quantitative procedures to measure the number and relative abundance of species, there is no universally accepted measure of the relative importance of different species in ecosystem function. This remains one of the principal outstanding problems in assessing the importance of biodiversity in ecosystem function.

The RSSD program primarily addressed questions regarding the function of savanna ecosystems and largely ignored the behavior of individual species. Yet the physical factors of climate and geology – such as rainfall, temperature, soil structure and soil nutrients – operating on individual organisms, as well as interactions between organisms, constitute the evolutionary forces that configure the characteristics of ecosystems. System properties such as productivity, structure and resilience are not under direct selection, but are modified as a result of changes in species populations and

their properties. All ecosystem properties are the result of a particular mix of species in time and space possessing a given set of characteristics. Therefore, the subtraction or addition of species from a savanna ecosystem ought to modify its structure and function at some scale. The interesting question is then at what scale, and by how much, are the properties of a savanna ecosystem modified when its species composition changes. We would also like to know the mechanism responsible for the changes.

Tropical savannas in different continents when growing under similar values of PAM and PAN exhibit very similar ecosystem properties in spite of being composed of an entirely different set of Linnaean species (Medina and Huber 1992). In other words, two savanna ecosystems can be functionally very similar even when their species composition is not. It is valid to conclude that in such cases convergence in the relevant species properties has taken place. The interesting question is therefore what those relevant properties are, and by how much do sets of species from different savanna ecosystems have to resemble each other to produce similar ecosystem characteristics.

Invasion of American and Australian savannas by African grasses, removal and/or reduction in the abundance of grass species through overgrazing, and the removal of shrubs and trees through intensification of fire regimes and mechanical means are examples of additions and removals of species that can be used to test the null hypothesis.

8.2   SAVANNA STRUCTURE AND FUNCTION

Ecosystem function can be interpreted in two ways. It can refer to the flow of energy and nutrients through an ecosystem or to the flow of species populations through time, i.e. the persistence of species populations and their properties, what Holling calls the resilience of the system (Holling 1973, 1986; Solbrig 1993). The usual way of looking at ecosystem function is to consider only the flow of energy and nutrients. We first discuss how species characteristics control the flow of energy and materials in the savanna ecosystem, and then address how species characteristics give the savanna ecosystem its resilience.

The herbaceous component of the savanna can be considered as the controlling element of the system and the one that regulates fundamental ecological processes such as water balance, productivity, mineral cycling, fires and herbivory. The common species have wide geographical distributions, yet each species has its own phenology and microdistribution (Solbrig *et al.* 1992). Although the herbaceous stratum is considered to be continuous, it is only so at the height of its growth, since the actual basal area of the grasses may be only 10–20% (Sarmiento 1984).

8.2.1 Dynamics of savanna resources

Water and nutrients are the basic resources that limit productive processes in tropical savannas. Soil moisture regimes, in turn, are affected by (1) the total amount and seasonal distribution of rainfall and the proportion of this water that enters the soil (2) the water-holding capacity of the soil, which is largely a function of soil particle size and depth, and (3) the amount of evapotranspiration, which is related in complex ways to climate, soil particle size, surface characteristics and the type of vegetation at the site. In turn, savanna community structure and species composition are highly correlated with soil-water dynamics along moisture gradients (Silva and Sarmiento 1976a,b).

Savanna soils vary widely in particle size, structure, profile and depth, reflecting the interaction of geology, geomorphology and climate, as well as the influence of topography, the kind of vegetation cover and animal activity (Young 1976; Montgomery and Askew 1983). Three factors play an important role in pedogenesis: topography, parent material and age.

The principal influence that topography has over the ecosystem is on the regulation of drainage, and ultimately over the water balance. In turn, through their action on pedogenesis, the agents that produce the relief indirectly determine the physico-chemical characteristics of the soils, so that relief also translates into the chemical and nutritional characteristics of savanna soils (Sarmiento 1984).

Dystrophic savanna soils derived from the weathering of acid crystalline rocks or from ancient sedimentary deposits generally have low reserves of weatherable minerals. The predominance in these soils of 1:1 lattice clays and iron and aluminum oxides results in low effective cation exchange capacity and small amounts of total exchangeable bases, particularly calcium and magnesium (Jones and Wild 1975; Lopes and Cox 1977; Mott *et al.* 1985). Phosphorous levels are sometimes also very low, and soils rich in sesquioxides have a high capacity for fixing phosphorous. Some highly weatherable soils also have high levels of exchangeable aluminum (Lopes and Cox 1977; Haridasan 1982).

The nutrient status of the soil in tropical savannas is related principally to the age of the sediments (Cole 1986). For example, in the Orinoco savannas, the poorest soils (oxisols and ultisols) are those derived from the oldest deposits, since these materials have been subjected to predogenic processes for prolonged periods of time.

With the exception of extremely acid soils, the amount of organic matter is the main determinant of cation exchange capacity. In wet savannas, high rainfall and an extended wet season favor plant production, with a consequent input of organic matter into the soil. Because of the almost yearly frequency of fire, the organic matter input is almost exclusively the result of below-ground production, since fire effectively mineralizes most of the aerial matter

produced (Sanford 1982; Menaut *et al.* 1985). High temperature and humidity favor microbial activity. However, microbial activity is limited by the low levels of assimilable carbon, high C: N ratios, lignin content, and, in some cases, high amounts of condensed tannins and secondary chemicals. Microbial activity may be stimulated by root exudates and by water-soluble compounds produced by earthworms (Lavelle *et al.* 1983; Menaut *et al.* 1985).

Mound-building termites, especially earth-eating species, modify the physico-chemical properties of the soil in their nests by selecting fine particles in their construction and by increasing the nutrient content of the soil in the nests, especially Ca, K, Mg and P, through their feeding activities (Pomeroy 1983; Lopez-Hernandez *et al.* 1989). Termites are efficient foragers and can denude the area surrounding their nests of organic matter and its nutrients. In the American savannas ants of the genera *Atta* and *Acromyrmex* behave in a similar manner to termites, removing litter from a large area and concentrating its nutrients in their underground nests. According to Coutinho (1984), a well-developed ant colony processes a ton of material in a year. Termites and ants create a patchy nutrient distribution that in turn is perpetuated by the vegetation, especially trees that grow preferentially on these mounds.

The nutrient dynamics of tropical savannas is now well known. Several authors (Medina 1982, 1993; Sarmiento 1984; Menaut *et al.* 1985) have summarized existing knowledge on nutrition partitioning between various compartments in the savanna ecosystem and proposed models for the cycling of nitrogen and other elements. The principal conclusion of these studies are that fire represents the principle source of nutrient loss from the system, that internal cycling accounts for the greatest proportion of nutrient fluxes, and that the most important compartment is the organic matter in the soil. The deficit in nitrogen must be covered through rainfall input and free-nitrogen fixation.

The flow of energy and nutrients through savanna ecosystems is tightly linked to the flow of water through the soil–plant–atmosphere continuum (Figure 8.2). Pulses of energy and nutrient input to the biotic components of the ecosystem result from pulses of production of plants. There are two levels of moisture pulses: (a) the alternation of dry and wet seasons, and (b) changes in PAM due to irregularities of rainfall during the wet season. In the wet neotropical savannas, there is an important distinction between savanna trees and grasses in this respect: grass production is tightly linked to the rainfall pulses whereas tree production is not (Sarmiento 1984; Cole 1986; Frost *et al.* 1986; Walker 1987). Trees rather depend on total annual rainfall to replenish underground water reserves. In contrast, in the drier, sandy savannas of southern African, trees seem to be depending on the rainfall pulses as do the grasses. In neotropical savannas, grasses represent a very high fraction of the total plant biomass, therefore most of energy and
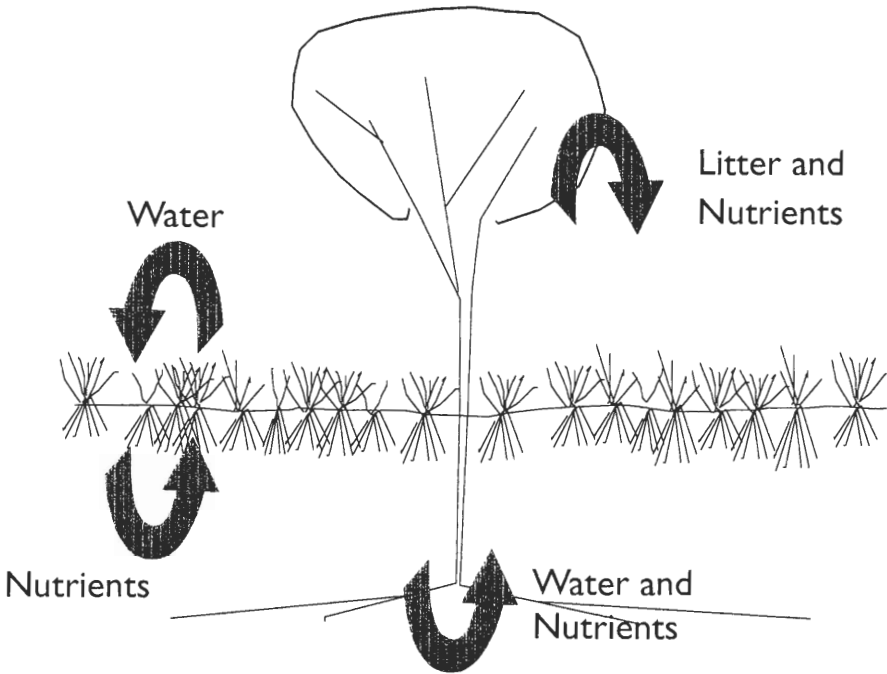
Litter and
Nutrients

Water

Nutrients

Water and
Nutrients

Figure 8.2 Nutrient cycling in savannas. The deep roots of trees obtain water and nutrients from the deep layers of the soil. Tree leaf and litter fall and decompose on the upper layers of the soil (upper 30 cm approximately) where they are utilized primarily by the grass layer. Some water and nutrients may percolate to lower layers, but it is insignificant compared to the pumping action of trees

nutrients flowing through the system are linked to the rainfall pulses. After several days without rain, soil moisture is reduced and not available to the grasses. The consequent closure of stomata and the loss of photosynthetic tissue if drought persists will reduce the uptake of carbon dioxide. The flux is reestablished as soon as it rains, and adequate soil moisture availability allows transpiration water fluxes from the soil to the atmosphere through the plants (Sarmiento *et al.* 1985).

A number of estimates of the productivity of tropical savanna grasses have been carried out. Most of these studies were made assuming that productivity, the gain of new organic matter by vegetation, approximated to the measured increase in above-ground biomass. However, this assumption has proved to be incorrect and has led to an underestimation of true productivity by a factor of two or three (Sarmiento 1984; Long *et al.* 1989, 1992) for three reasons: (1) below-ground production can be as high or

higher than above-ground biomass; (2) the methods used assumed that death of tissues occurs only after the peak of production has been reached; (3) the researchers did not consider that different species reach their peak of production at different times. Recent studies (Table 8.2) in tropical grasslands that took these considerations into account have obtained values that are 5–10 times higher than those from previous studies, and an approximate figure of 1000 to 2300 g m^{-2} year^{-1} for tropical forests (Ajtay *et al.* 1979).

An accurate appraisal of tropical savanna productivity is essential to understand the input of organic matter into the ecosystem and the amount and material available for producers and decomposers, including those in

Table 8.2 Estimates of productivity of tropical savanna grasses

Site	Apn[1]	Bpn[2] (gm^{-2} yr^{-1})	Pn[3]	Rainfall (mm)	Source of data
Fete Ole (Senegal)	82	–	–	209	Singh and Joshi (1979)
Pilani (India)	217	61	278	388	Kumar and Joshi (1972)
Welgevonden (S. Africa)	710	–	–	388	Singh and Joshi (1979)
Nairobi National Park (Kenya)	1071			460	Desmukh (1986)
Serengeti (Tanzania)	520	–	–	~700	Bourliere and Hadley (1970)
Jhansi (India)	1014	524	1538	~700	Shankar *et al.* (1973)
Kurukshetra (India)	2407	1131	3538	790	Singh and Yadava (1974)
Nairobi National Park (Kenya)	805	1075	1880	800	Long *et al.* (1992)
Nairobi National Park (Kenya)	3228	–	–	850	Cox and Waithaka (1989)
Rwenzori National Park (Uganda)	730	1572	2302	900	Strugnell and Piggott (1978)
Calabozo (Venezuela)	369	–	–	1022	Medina *et al.* (1977)
Ban Klong Hoi (Thailand)	1568	468	2036	1077	Long *et al.* (1992)
Barinas (Venezuela)	604			1093	Sarmiento and Vera (1977)
Mokawa (Nigeria)	614	–	–	1115	Ohiagu and Wood (1979)
Lamto (Ivory Coast)	498	–	–	1158	Singh and Joshi (1979)
Olokemeji (Nigeria)	680	–	–	1168	Hopkins (1968)
Lamto (Ivory Coast)	830	1320	2150	1300	Menaut and Cesar (1979)
Lamto (Ivory Coast)	1540	2040	3580	1300	Menaut and Cesar (1979)

[1] Apn – Above ground primary productivity
[2] Bpn – Below ground primary productivity
[3] Pn – Total productivity

the soil. Such knowledge is also necessary to understand the potential effect of removal of vegetation as a result of fire, herbivory and human activity. The new values indicate that the efficiency of light conversion in tropical savanna grasses is higher than previously estimated, which is of economic importance. Finally, an accurate assessment of tropical savanna productivity is indispensable to establish a baseline against which the effects of future changes in global CO_2 levels may be assessed.

8.2.2   Demographic and physiological characteristics of savanna species

To understand the ways in which savanna species respond to natural stresses and human disturbances, account must be taken of the existence of a great diversity in life history characteristics and physiology among savanna species. Many different species with apparently similar characteristics can coexist in the same community. However, their patterns of growth and reproduction are different (Sarmiento and Monasterio 1983). Some grass species in wet savannas start to grow with the first rains or shortly after a late fire, and after a spurt of growth go into a reproductive phase. Others grow more gradually, develop their shoots slowly, and enter into their repro-ductive phase towards the middle or the end of the rainy season. This temporal displacement in the peaks of growth and reproduction may partly explain the ability of species which superficially are very similar in morphology to coexist in the same environment.

The soil-available moisture and soil-available nutrients are not the same in the early, middle and late season (Sarmiento 1984), which suggests that early, middle and late species may have different physiological capabilities. Preliminary studies by Goldstein and Sarmiento (1987) indicate that each of the phenological groups, but especially early bloomers, have different ecophysiological attributes, and that these differences are of adaptive value. Precocious and early growers tend to maintain lower transpiration rates, have higher water-use efficiencies (ratio of carbon assimilated to water loss) and higher turgor pressures than intermediate and late-growing species. So, for example, *Leptocoriphium lanatum*, a precocious species, showed maximum daily transpiration rates of 7.5 nmol m^{-2} s^{-1}, compared with 12 nmol m^{-2} s^{-1} for *Trachypogon vestitus*, a late species. Maximum photo-synthetic rates at high photon flux densities and low vapour pressure densities are between 25 and 32 µmol m^{-2} s^{-1} and do not differ significantly among species (Goldstein and Sarmiento 1987). Maintenance of positive turgor pressure should allow the precocious species to maintain continuous growth under high water-stress conditions. The observed differences in gas exchange characteristics could explain the high growth rates of the preco-cious species during the transition from the dry to the wet season. The differences in ecological behavior among perennial C4 savanna grasses may also be determined by other traits related to growth and morphology such

as the proportion of photosynthate allocated to leaves and underground organs. The higher initial growth rates of the early-growing species may also be strongly associated with the higher proportion of photosynthate and nutrient reserves allocated to roots and below-ground organs (Medina and Silva 1990). At the end of the dry season growth may be supported more by stored nutrients and carbohydrate reserves than by current absorption. Early growers may behave as stress-tolerant species and be rapidly out-competed when nutrient and water availability increases. Studies by Raventós and Silva (1988) show that late growers are competitively superior to early growers during the wet season.

Herbaceous and shrubby nitrogen-fixing Leguminosae are an important floristic component of savannas, particularly in South America. However, they frequently contribute less than 1% of the total biomass of the herbaceous layer. Yet in nitrogen-deficient savannas these species play an important role in nitrogen cycling, covering a substantial fraction of the nitrogen losses caused by fire (Medina and Bilbao 1991).

8.2.3   Species diversity and ecosystem stability

While definitions of stability have previously carried implicit assumptions of an equilibrial or steady state as a preference point, more current definitions of stability recognize that a range or cloud of system states may be used for reference (Solbrig 1993). That range may contain regular cycles at different temporal scales, threshold responses and apparently chaotic behaviors with underlying order (e.g. "strange attractors"). When cycling among system states is a characteristic system behavior it becomes essential to differentiate measures of short- and long-term stability, because while a short-term measure may indicate instability, a longer-term measure may indicate stability. While savannas may oscillate or fluctuate among a range of states, they can still be stable systems.

Measures of stability that are based upon floristic composition may provide different results than measures based upon functional group compositions owing to similarity of function of species within a functional group. The more alike species are in their functions, the less critical it is to maintain a particular species, as long as all critical ecosystem functions are preserved. Thus, the level of functional identity within groups must be known in order to interpret the significance of changes in floristic composition.

Resilience, that is the capacity of the system to maintain its overall functional identity, is dependent on the ability to withstand unusual combinations of environmental factors, usually called disturbances. These may be the result of extreme values of an otherwise natural event, such as an extremely dry year, an intensification in the frequency of fires, or fire suppression, where fire is a regular event, or they may be the result of an entirely new circumstance, such as the appearance of a new pathogen or

herbivore. There are several important modifiers of disturbance responses. These modifiers must be taken into consideration to interpret species responses accurately. They are (1) time since disturbance, (2) direct and indirect interactions among species following or preceding the disturbance, (3) abiotic variables such as soil depth, soil fertility or rainfall, and (4) the occurrence of other regular events causing mortality, such as fire.

In particular, time-dependent variables such as rainfall may confound responses to disturbance. When rainfall changes over time since a disturbance, the effects of the change in rainfall must be disentangled from the effects of the disturbance in order to interpret the response. It is important to recognize that the response of the savanna to a disturbance depends upon the initial state of the system. In other words, system dynamics are sensitive to initial conditions. The history of disturbance also has an important impact, through selective forces, upon the presence of species that are adapted to subsequent disturbances of the same kind. Indeed, savannas may be intrinsically stable relative to other systems because they have evolved with habitual fires, herbivory and drought. Thus, the continued persistence of savannas may necessitate their presence to preserve stability.

8.3   A MODEL OF SAVANNA FUNCTION

The one common feature of all tropical savannas is climatic seasonality. The rhythm of the wet and dry seasons regulates the rhythm of growth and reproduction of the herbaceous and woody vegetation. This rhythm is driven by two major factors: rain and fire (Fig. 8.3). Fire, taking place towards the end of the dry season, generates two pulses: increased nutrient availability and high PAR radiation at ground level, both favorable to grass growth. The onset of rains represents the third pulse. With the onset of the rainy season the upper profile of the soil slowly gets saturated, depending on the amount of rainfall, local topography and soil properties. Plant growth progresses rapidly mostly from the regrowth of perennial grasses, but also from the germination of their seeds (Fig. 8.3).

Although contrasting, wet and dry seasons are not totally homogeneous intervals of time, but are yearly oscillations in PAM and PAN that in turn regulate the growth rate, that will then affect the light regime within the canopy and the amount of standing live and dead biomass, that in turn affects the probability of fire. The large number of coexisting herbaceous and woody species are in part adaptive responses to the seasonal changes in the values of PAM, PAN and light that circumscribe different niche spaces utilized by species with different morphologies, physiologies and life histories. For example, since the PAM and PAN status is more favorable near ground level, early-growing species will have primarily superficial roots, low stature and globose form.
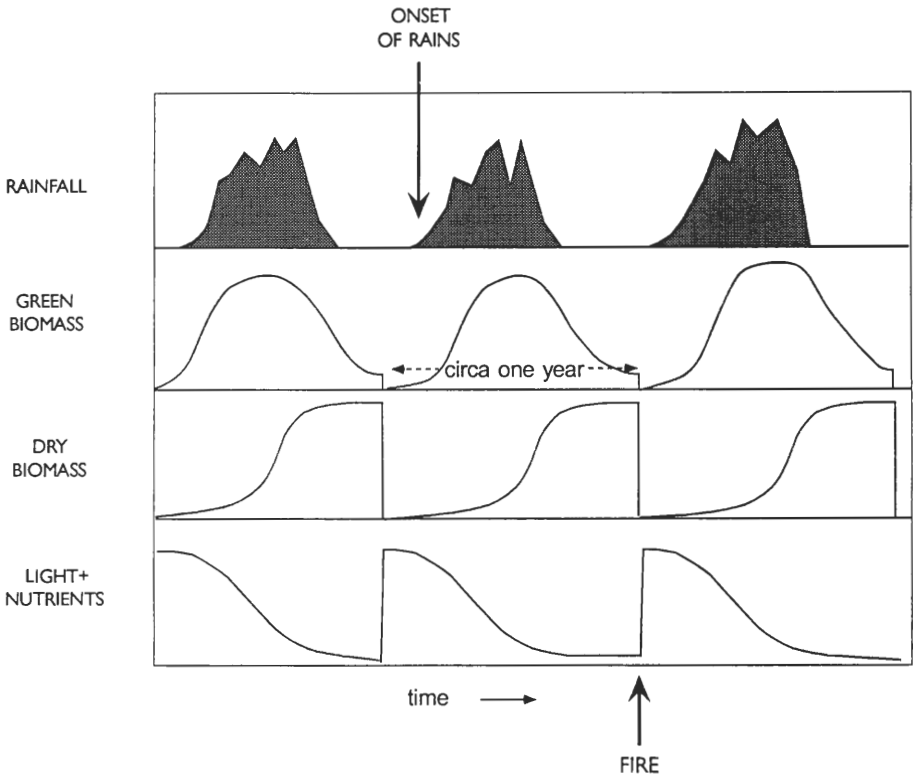
Figure 8.3 Diagram showing the coupling of the seasonal rhythms of green biomass, dry biomass, nutrient and light availability at the ground level with the two main factors of savanna functioning: rainfall and fire

As the season progresses, PAM in the upper layers of the soil becomes more favorable, but PAN less so, as more nutrients are removed by the growing vegetation. Roots of species initiating growth after the precocious ones will grow deeper into the soil. Also, the increased biomass changes light conditions within the canopy, which in turn reduces tillering and promotes elongation of existing tillers (Deregibus *et al.* 1985). Light conditions at ground level become unfavorable for seedling germination and growth. Late-growing species move their photosynthetic surface upwards, as the tillers elongate and the basal leaves senesce and decompose. Their seeds show dormancy, which has evolved through natural selection as any seedling that has no dormancy and germinates late in the season will produce seedlings that cannot attain the minimum size necessary to withstand the dry season before the end of the rainy period and dies (Silva and Castro 1989).

Towards the end of the rainy season, PAM again deteriorates as rainfall

becomes more scattered, but the accumulation of litter and dead under-
ground biomass leads to an improvement in PAN. Light environment within
the canopy is now very poor for growth as the canopy has reached its
maximum extent. Savannas differ in phenological diversity, with some
groups becoming extremely dominant whereas other groups may be totally
absent. Some results show that this variation is related to factors such as
rainfall and soil which determine the length of the season with available
moisture (Sarmiento 1983).

In addition to the phenological differences, grass species belonging to
different tribes exhibit differences in their photosynthetic types. Most
tropical savanna grasses belong to the Paniceae, Andropogoneae or Chlori-
deae and exhibit a C4 type of photosynthesis. However, some savanna grass
species exhibit the C3 photosynthetic type, especially those growing in hyper-
seasonal savannas (Medina and Motta 1990). Because of their better forage
quality, such species are of great importance (Klink and Joly 1990). C4
grass species, in turn, can be divided into malate and aspartate formers. The
former grow preferentially in humid savannas with dystrophic soils, while
the latter dominate in dry and semi-dry seasonal savannas (Medina and
Huber 1992; Baruch and Fernández 1993).

Trees are an important component of savanna ecosystems. Tree species
from different savannas and different continents differ in their morphological
and physiological characteristics. In wet neotropical savannas trees tend to
be evergreen, have relatively high root/shoot biomass ratios and large,
highly sclerophyllous leaves. Their roots usually explore deeper soil horizons
than grasses, and therefore in wet savannas are exposed to more uniform
water levels. Transpiration rates are generally high even during the dry
season, and leaf water potentials are maintained above the turgor loss point
because of sufficient soil water availability and the hydraulic properties of
the vascular system (Goldstein *et al.* 1990). In dry savannas with more
fertile soils deciduous trees are the norm, making it difficult in these
savannas to separate attributes that enhance a tree's capacity to withstand
water stress from those that ameliorate nutrient stress.

The principle difference between trees from different savannas is in the
length of their active season and the degree of xerophytism they exhibit. In
wet oligotrophic savannas with water available in the subsoil, evergreen trees
with an extensive deep root system and scleromorphic foliage predominate
(Walter 1973; Sarmiento *et al.* 1985). In environments with a relatively
extended wet season and rich soils, trees with large deciduous leaves and
relatively small and superficial root systems dominate and in semi-arid
savannas, trees with small, scleromorphic leaves are the norm. These differ-
ences have been explained in terms of water and nutrient economy (Medina
1982; Sarmiento *et al.* 1985).

A complicating factor is nutrient economy. Very wet savannas occur
mostly over highly oligotrophic soils. The scleromorphic characteristics of

leaves in trees from oligotrophic savannas may be an indication of nutrient deficiency, rather than water economy. It has been suggested (Sarmiento *et al.* 1985) that the large leaves of savanna trees growing on oligotrophic soils have evolved as a mechanism for augmenting transpiration and thereby increasing nutrient uptake.

8.4   EFFECT OF SPECIES DIVERSITY ON ECOSYSTEM FUNCTION

We now explore how changes in species diversity affect ecosystem function in order to test our null hypothesis. For this purpose we make use of natural and unplanned human experiments involving the addition and/or removal of plant and animal species from natural savanna ecosystems.

8.4.1   Invasion of South American and Australian savannas by African grasses

Several species of African grasses (such as *Hypharrenia rufa*, *Melinis minutiflora* and *Panicum maximum*) have become naturalized in the South American llanos and cerrado and in the Australian savannas. A number of important functional differences exist between African invaders and native grasses. Thus, there are many possible functional outcomes that may arise at the ecosystem level as a result of the establishment of these species in American and Australian savannas, through their effects on herbivory, hydrology, decomposition and nutrient cycling. Invaders may also initiate new successional processes due to their effects on abiotic and biotic processes. First it must be demonstrated that the invasions are promoted by absolute differences in competitive abilities and not by disruptions in nutrient cycling, which in turn result from the removal of native species by human activities. Indeed, most invasions in South America have followed such primary disturbance of the soil and vegetation, and there is evidence that the invaders may not persist unless these anthropogenic disturbances continue. Furthermore, results from long-term fire exclosures in Venezuela demonstrate that African invaders are not as tolerant of fires as South American species, possibly owing to the greater fuel accumulations they produce over long fire-free intervals. There is evidence from the Serengeti in East Africa that communities of native species growing on disturbed areas such as termite mounds, excavation mounds made by digging mammals, etc, are highly resistant to invasion by exotics. While this may suggest that there may be differences among savannas in invasive resistance, there were invasions by exotic species along roadcuts in the Serengeti.

In Venezuela, African species are displacing native species from many

savanna areas. *Hyparrhenia rufa* is very abundant in the lowlands, while *Melinis minutiflora* is more prevalent in cooler and wetter uplands. According to Baruch (1986) and Baruch *et al.* (1985), the African species are displacing the native ones because of their greater photosynthetic rate and accompanying growth rates under favorable soil water conditions. They found that African species had higher photosynthetic rates than native species when soil water potentials were above 1.5 MPa, reaching maximum rates of 31 μ CO_2 m^{-2} s^{-1} under the most favorable water conditions, as compared with only 27 μ CO_2 m^{-2} s^{-1} for the native species. On the other hand, growth and photosynthesis ceased in the introduced species at soil water potential of -5.6 MPa, while native species could function until the soil water potential reached -6.9 MPa. According to Baruch this explains why native species are not displaced from the drier sites.

The mineral content of native grasses is in general lower than that of introduced grasses (Medina 1987, 1993; Klink, 1992) especially P, Ca and N. The low nutrient content of the native species constrains their productive capacity. Furthermore, they also respond less to fertilization treatment. These results indicate that the nutritional requirements of the introduced African grasses may not be met in undisturbed American and Australian savannas. According to Bilbao and Medina (1990), African species are able to invade because of their increased rate of mineralization of organic matter following a disturbance such as increased fire frequency and the introduction of cattle. Furthermore, the higher efficiency of nitrogen use allows the African species to produce more biomass under these conditions.

The conclusion from these studies is that although African grasses are replacing native grasses under the influence of anthropogenic disturbances in Australia and South America, they are not functionally identical to the species they replace, and that consequently they have a significant effect on ecosystem function. This would disprove the null hypothesis.

8.4.2   Species changes resulting from fire exclusion

Experimental exclusions of fire produce significant changes in vegetation structure: primarily an increase in the density of woody elements, but also changes in species composition and the relative abundance of different species (Braithwaite and Estbergs 1985; Frost and Robertson 1987; Lonsdale and Braithwaite 1991; San Jose and Fariñas 1991; Dauget and Menaut 1992; Moreira 1992). Herbaceous species are affected less by fire itself than by the timing of the fire. In south and east African savannas, annual burning increases the abundance of *Themeda triandra, Digitaria pentzii, Pogonathria squarrosa* and *Heteropogon contortus*, whereas fire exclusion favors *Cymbopogon plurinodis, Sporobulus fimbriatus* and forbs (Frost and Robertson 1987).

The actual effect of these changes on ecosystem function are not easy to evaluate. Increases in woody species undoubtedly modify the nutrient dynamics and productivity in wet savannas, owing to differences in phenological behavior and litter quality. Many studies have shown that fire has an effect on productivity and aerial and below-ground biomass. So, for example, Singh (1993) found that burning increased the mean annual canopy and below-ground biomass of a dry tropical savanna by 40% and 12% respectively, and produced an increase of 24% in mean above-ground net production and 9% in mean below-ground net production with respect to control. Mean annual above-ground and below-ground net primary production were 471 and 631 g m^{-1} in control, and 584 and 688 g $^{-2}$ in burned savanna, respectively. However, these changes were not related to species changes but were the direct result of changes in nutrient cycling.

Clearly there is a marked change in savanna functional properties, but it is more difficult to state that it is due to changes in species composition and not to changes in the physical properties of the soil as a result of the fire. It is less clear whether the null hypothesis is disproven in this case.

8.4.3   Species changes resulting from herbivore introduction or exclusion

Large vertebrate ungulate herbivores modify the chemistry, morphology, productivity and distribution of savanna plant species through their effect on the physical and chemical plant environment and on nutrient cycling (Ruess 1987). In the last three hundred years cattle have been introduced first into the South American savannas and in the last century into the Australian savannas, while African savannas have seen a reduction in their ungulate faunas resulting first from the introduction of rinderpest, and then due to various anthropogenic influences, including hunting. At the same time in certain protected areas ungulate herds have increased. These changes provide an additional test of the general hypothesis.

There is no question that fluctuations in ungulate populations affect ecosystem composition. Increases in cattle in Australia, that historically had no large ungulates, have produced significant changes in the composition of the grass flora (Mott et al. 1985). The extensive use of native pastures in the first 100 years after cattle were introduced into the state of Queensland in the 1840s led to the replacement of palatable species of grasses by less palatable ones (Mott et al. 1985). Although no precise list of the original species composition of the Queensland savannas exists, the consensus among botanists is that in the tall grass eastern region of Queensland and in the interior valleys, "kangaroo grass" (Themeda australis), a good forage grass, was replaced by "black spear grass" (Heteropogon contortus), a species of lower forage quality, due to overgrazing and indiscriminate burning (Burrows et al. 1988). Heteropogon contortus and Themeda australis

are both short-day plants and are early bloomers in the subtropical tallgrass regions, with similar responses to fire and nutrients and reproductive capacities (Mott *et al.* 1985). *Themeda australis* produces longer-lived tussocks with poor regeneration (average life over 9 years) than *H. contortus* (average life ± 5 years) which shows better regeneration. Despite these differences, there is no indication of major changes in productivity or nutrient cycling following the species displacement. At least at the ecosystem scale the change in species composition had no effect on the functioning of the system, and this appears to be an indication of its resilience at this scale.

In South African savanna grasslands, O'Connor and Pickett (1992) found that species composition was affected by grazing history. Lightly grazed sites were characterized by the longer-lived, palatable perennials. *Themeda triandra, Bothriochloa insculpta, Heteropogon contortus* and *Digitaria eriantha*, and heavily grazed sites by the short-lived perennials *Urochloa* spp., *Sporobolus nitens, Chloris virgata* the unpalatable *Aristida bipartita* and some forb species. Yet models of population growth of lightly and heavily grazed ecosystems showed that rainfall and not grazing had the greatest effect on population growth, which contradicts other observations (O'Connor and Pickett 1992).

The changes in species composition brought about by herbivory are more subtle than those brought about by fire or the introduction of African grass species. Although there are no major short-term changes in savanna function, thereby upholding the null hypothesis, there are likely to be long-term changes. In effect, in all cases species favored by herbivory have shorter life cycles than those they replace. This should affect savanna resilience and its ability to resist other types of perturbations.

In dry savannas, herbivory affects the relation between the grass and tree layers, thereby drastically affecting savanna function. So, for example, in an arid steppe of southern Ethiopia, Billé (1985) reported a significant increase in the density of trees from 834 to 1710 individuals ha^{-1}. Likewise, in the subtropical savannas of the dry Chaco in northern Argentina, the introduction of cattle at the end of the last century has produced a visible deterioration of the vegetation, with the virtual disappearance of the grass layer and its replacement by introduced spiny shrubs and cacti, as well as an increase in two species of rodents (Bucher 1987). Unfortunately, no ecosystem level studies exist, so that ecosystem changes must be inferred. The disappearance of the grass layer modified the vegetation from a savanna into a scrub forest, and undoubtedly represents the lack of resilience of the Chaco system to the disturbance represented by the introduction of cattle. On the other hand, Pandey and Singh (1992a,b) in controlled experiments, have shown that in a dry tropical savanna in India, grazing increases species diversity, specifically an increase in the number of annual grasses and forbs in relation

to permanently protected plots. Many researchers consider these savannas as non-representative of tropical savannas.

In wet oligotrophic savannas, ranching does not result in bush encroachment. Rather, because of the increased frequency of burning by ranchers anxious to encourage early resprouting of savanna grasses, woody species are likely to decrease with ranching. In dry savannas with relatively good nutrient levels and good forage quality, overgrazing significantly reduces the grass layer and standing dead biomass during the dry season. This reduces fire frequency and allows the encroachment of unpalatable woody species that eventually displace the herbaceous vegetation. In the nutrient-poor oligotrophic savannas, low-quality forage does not allow a very high animal load so that fuel load is not reduced significantly, permitting yearly or other-yearly fires that reduce the establishment of woody species. This is confirmed by studies conducted in the Argentinian Chaco (Morello and Saravia 1959; Morello 1970). If grass is permitted to establish, and cattle are not allowed to roam freely but are removed when the grass species bloom and fruit, encroachment by woody species is controlled, and both primary and secondary productivity increases.

8.4.4 Changes resulting from increases or removal of trees and shrubs

Mechanical removal of shrubs and trees is practiced in some savanna areas in order to increase grass production for cattle. The removal of the woody layer produces changes in soil characteristics and nutrient cycles that have ☀ been documented for South Africa and Australia where this practice seems to be widespread (Gillard *et al.* 1989; Teague and Smit 1992). Removal of ☀ trees and shrubs, however, can result in a decrease in species establishment (Belsky *et al.* 1989). Whether the effect of tree removal on grass growth is positive or negative is not related to the type of tree species, but to the available moisture.

Tree–grass interactions involve competition for water and light. Tree litter can increase organic matter and soil nutrient content significantly. Grass roots are more abundant than woody species roots in the upper layers of the soil. This is true even for shallow-rooted trees such as the African *Colophospermum mopane* (Dye and Walker 1980).

Grasses and woody species have different phenological and demographic behavior and a different water and nutrient economy. They constitute two distinct functional types, reinforcing the belief that species changes will significantly affect ecosystem function and resilience only when an entire ☀ functional group is lost. So, for example, Isichei and Muoghalu (1992), studying the effect of tree canopy cover on soil properties in a Nigerian savanna, found that soil under tree canopies has significantly higher levels of organic matter, calcium, magnesium, potassium, total exchangeable bases,

cation exchange capacity and pH than soil in open grasslands. The loss of ⋇
either the grasses or the trees in this situation could lead to significant
changes in ecosystem function.

8.5   RESILIENCE AND ECOSYSTEM FUNCTION

A number of ecosystem characteristics can be used to measure ecosystem
resilience, from vegetation structure to productivity. At the broad scale
employed in this analysis, the biggest change in ecosystem function was
detected when woody species increased at the expense of grasses, or vice
versa. In such instances, changes in structure and standing biomass are very
evident. This is the case when the fire regime or the degree of large ungulate
herbivory changes, or when woody elements are removed mechanically.
Replacement of one species of grasses by another, or a species of tree by
another, seems to have a much smaller effect on structure, productivity or
standing biomass. Yet, when detailed studies are performed, changes in
ecosystem function are inevitably encountered.

In every case, even at the level of functional group, the measured changes
are complex and strongly influenced by environmental factors such as preci-
pitation and fire. Resilience appears to be intimately connected to ecosystem
function. When changes in function brought about by a disturbance are
minor, the system has the ability to recover. The null hypothesis does not
appear to be upheld by the evidence. Every savanna species appears to have
unique physiological and demographic characteristics (Silva 1995), but it is
these species differences, through changes in the relative abundance of
species as a result of disturbances, that given savannas their resilience. In
other words, because every savanna species is functionally and demographi-
cally unique, savannas are able to persist in time. This, in our opinion, is
the significance of species diversity.

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