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2.1 Introduction

Tropical savannas, defined as ecosystems formed by a continuous layer of graminoids (grasses and sedges) with a discontinuous layer of trees and/or shrubs, are the most common vegetation type (physiognomy) in the tropics. Tropical savannas are found over a wide range of conditions: rainfall from approximately 200 mm to 1500 mm a year, temperature from subtropical regimes such as the South American Chaco and the South-African savannas with temperature seasonality and cold-month average temperatures below 10 °C, to low-latitude savannas with no temperature seasonality, and soils from volcanic soils such as in parts of the Serengeti plains in Tanzania to dystrophic soils such as in the Brazilian cerrados. The one constant climatic characteristic of tropical savannas is rainfall seasonality. Yet the duration of the dry season can vary from 3 to 9 months, with a mode of 5 to 7 months.

Savannas can be subdivided into a number of savanna types (Table 2.1; Sarmiento 1984) based on rainfall, seasonality characteristics, and density of woody vegetation. These types are not always persistent in time, and natural and anthropogenically induced changes in climate, in nutrients, in fire regime, and in herbivory, can displace the borders of the areas occupied by the various types of savanna vegetation, and the borders with other types of vegetation: humid forests and semideserts. A good example is provided by the border between the Brazilian savanna known as the cerrado and the tropical forest. It is well documented (van der Hammen 1989; Furley et al. 1992) that during the Pleistocene dramatic expansions and shrinkage in the extent of the cerrado took place.

Table 2.1. Physiognomic types of savannas (Sarmiento 1984)

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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) Shrub and or trees isolated 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 higher 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 to 15%: *tall savanna woodland*.
 - c) Tree cover 15 to 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*.
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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; Cole 1986; Medina and Huber 1992). From a floristic point of view, savannas from different continents are quite distinct and show more similarities with other local vegetation types than with savannas in other continents. So, for example, the phylogenetic affinities of the flora of the Brazilian savannas known as *cerrado* are with the Amazonian flora, rather than with the flora of West Africa; however, physiognomically, the *cerrado* is more similar to the savannas of West Africa than to the Amazonian forest. In turn, African savanna vegetation types are floristically more related among themselves than they are with savanna vegetation in other continents. The conclusion is inevitable: the biota of different savannas are the result of convergent evolution from different floristic and faunistic stocks. As such they provide an interesting puzzle for the evolutionary ecologist: to identify the selective forces that create this unique and widespread tropical physiognomy.

Savanna ecologists have emphasized the similarities rather than the differences in savanna ecosystems. 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 to explain the function of tropical savannas (Frost et al. 1986; Walker 1987; Sarmiento 1990; Werner 1991). They 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, and (4) herbivory. These determinants are predicted to 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 determinants of savanna structure at the higher scales. They circumscribe what was called the PAM-AN plane. Where PAM and PAN have high values, woody elements dominate, and as PAM and/or PAN increase eventually the savanna gives way to a moist forest. When PAM and/or PAN have very low values, xerophytic elements prevail, and if the values of the PAM-AN plane get very low, the savanna is replaced by a semidesert. Between these 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 have a savanna and not a semidesert 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, are supposed to determine the density of the tree layer, the productivity of the system, and the rates of nutrient and water flow through the system.

Savannas are very heterogeneous systems in which small forests along streams and moist areas and scattered trees are interspersed in a sea of graminoid-dominated vegetation. So, for example, in the savannas of the Orinoco, the density of the woody vegetation varies with soil depth (PAM) and with the age of the deposits (PAN) (Silva and Sarmiento 1976). Experimental exclusion of fire or herbivores (mostly introduced cattle) produces significant changes in vegetation structure, primarily an increase in the density of woody elements, but also changes in species composition (Braithwaite and Estbergs 1985; Frost and Robertson 1987; Lonsdale and Braithwaite 1991; San Jose and Fariñas 1991; Moreira 1992).

The RSSD program addressed primarily questions regarding the function of savanna ecosystems and ignored somewhat, but not entirely, the behavior of individual species. Yet 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 shape 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. What is so intriguing is that 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 different Linnaean species. The question then is not whether ecosystem properties are modified when species change, but how and by how much. The objective of this book is to address explicitly the role of species diversity rather than environmental factors in the function of tropical savannas.

In assessing the role of biodiversity on the function of savanna ecosystems, our first task is to define clearly what we mean by biodiversity in this context. Next, we emphasize the system nature of our approach. Savanna function and structure are two interrelated aspect of the savanna *system*.

2.2 Definition of Biodiversity

"Biodiversity is the property of living systems of being distinct, that is different, unlike. Biological diversity or biodiversity is defined as the property of groups or classes of living entities to be varied. Thus, each class of entity - gene, cell, individual, population and by extension species, communities, and ecosystems - have more than one kind. Diversity is a fundamental property of every living system. Because biological systems are hierarchical, diversity manifests itself at every level of the biological hierarchy, from molecules to ecosystems" (Solbrig 1991b). Here we concern ourselves primarily with species diversity.

The number of different kinds of species living today is enormous, although the exact number is not known with precision. Because taxonomists specializing in different phylogenetic groups have worked in great isolation, not even the exact number of described species is established. They are considered to be approximately 1.6 million. The total number of living species is estimated at between 10 and 30 million, with some computations being as high as 90 million. The exact meaning of all this variation is not known. Two explanations exist, but there is not enough evidence to disprove either. The classical view, held mostly by systematists, physiologists, ecologists, and other organismic biologists, is that processes, such as selection and competition, mold each species to function harmoniously with those surrounding them. In this view, life resembles a machine, a primitive one that does not require very precise parts, but an entity where most parts play designated roles. The other, more recent theory, which is most prevalent among physicists, molecular biologists, geneticists, and mathematicians, sees biodiversity as the manifestation of the dynamics of complex, nonlinear systems, far from equilibrium. For them, life is like a whirlwind in the desert that picks up a lot of dust and materials and arranges it briefly in what for an observer is a defined structure, but where the exact position of each particle is of no significance for the whole.

Neither of these views is entirely correct, nor are they entirely wrong. There exists an enormous body of evidence that indicates that most characteristics of species are adaptive, that is, that they enhance the Darwinian fitness of the individual. Yet there is overwhelming evidence that indicates that not every character is necessarily adaptive, and consequently no species is *optimally* adapted, i.e., possesses the suite of characters that gives it maximal fitness because of the existence of biological processes with a strong random component, such as mutation, and the various environmental factors that produce mortality. Therefore, according to the emphasis put by researchers in their studies, and the scale at which these studies are conducted, the deterministic or the random component of evolution is stressed.

An interesting evolutionary phenomenon is the existence of phylogenetically unrelated biotas with very similar functional properties and a suite of morphologically related species, such as temperate deserts or tropical savannas. The accepted explanation for this situation is that the morphological similarity of the species is the result of convergent evolution under similar selection pressures (Orians and Solbrig 1978). However, since the characteristics of the species in convergent systems are not identical, it is essential that clear predictive hypotheses be formulated indicating in what ways and in which characters convergent species should resemble each other. Otherwise, the fallacy of circularity can be incurred by attributing all similarities to convergent evolution, and all differences to differing phylogenetic histories.

Tropical savannas appear to be convergent in the above sense, even though phylogenetic relations among its species are present. The principal tropical savannas are found in Gondwanian continents: South America, Africa, India, and Australia. Consequently, there are some phylogenetic relations especially at the family level and to a lesser extent at the genus level. There are also differences in the degree of phylogenetic similarity between woody and herbaceous elements, the former being less similar in savannas from different continents, the former more. Therefore, when postulating convergent evolution, care must be taken to exclude the effects of common ancestry.

Compared to tropical rain forests, American savannas are poor in species. On the other hand, the African savannas (Menaut 1983) are almost as rich in species as the African rain forests. This may reflect the species poverty of the African rain forest more than the species richness of the African savannas. Australian savannas have more species than adjacent wet forests which are of limited extent in Australia. When compared to temperate grasslands and dry woodlands, tropical savannas are rich in species. Yet there is no complete inventory of the number of species in any tropical savanna. Best known are vascular plants, birds, and mammals; least known are invertebrates, especially non arthropods, fungi, and protists.

The similarity of tropical savannas is predicated primarily on the basis of the vascular vegetation, specifically the presence of a continuous layer of grasses, with or without a discontinuous layer of trees. However, the gramineae are a very stereotyped family of angiosperms, and the characteristics of savanna grass species cannot be necessarily attributed to convergence evolution.

2.3 Savanna Plant Species and Adaptive Strategies

Given that savannas in different continents have very few common species, especially among the woody elements, the similarity in function of different savanna ecosystems implies similarity in function of its different species. Unrelated species with similar functional characteristics are classed as *functional groups*. (Whittaker 1956, 1975; Walter 1973; Grime 1979; Schulze 1982; Körner 1993). Although the concept of functional group can be very useful, it presents serious practical problems. Linnaean species represent groups of similar breeding populations capable of interbreeding, and are consequently nonarbitrary evolutionary units. There is, however, no such nonarbitrary criterion to erect functional groups. The same species may be classed in different functional groups, according to the criterion adopted, since functional groups include all species that share a particular characteristic viewed by the ecologist as important. So, for example, all green plants can be classed as primary producers, all vegetable-consuming organisms as herbivores, and so on. These same species can then be classed as xerophytic or mesophytic according to their water requirements, or they can be classed as drought evaders, or drought endurers, and so on.

A less arbitrary concept to express functional similarity of species is that of *adaptive strategies* (Harper and Ogden 1970; Stearns 1976; Solbrig 1982). The concept of adaptive strategy is based on the notion that species are under constant selective pressure to increase their fitness, and that there are only a limited number of ways in which this can be done on account of developmental constraints (Solbrig 1993). In describing an adaptive strategy, the researcher must postulate the selective forces, as well as the developmental constraints that are responsible for the existence of unrelated species with similar functional characteristics. An adaptive strategy is a hypothesis to explain why a group of species shares certain characteristics. Use of the concept of adaptive strategy forces a greater scientific discipline than arbitrarily classifying species on the basis of shared characteristics, and this explains our preference.

2.4 Species Strategies in Relation to Plant-Available Moisture, and Plant-Available Nutrients

Plants compete for light, water, and nutrients. In savannas, competition is primarily for water and nutrients. There are at least four basic growth forms that have evolved in response to drought: (1) the drought-escaping ephemeral or deciduous perennial; (2) the deep-rooted phreatophyte; (3) the drought-enduring evergreen; and (4) the drought-resistant succulent (Stocker 1968; Barbour 1973; Solbrig 1986; Schulze and Chapin 1987). A drought-escaping plant is one that is active only in the wet season, and survives the period of drought stress as seed or by going dormant; a drought-enduring species is one that continues being physiologically active during the period of drought as long as there is sufficient soil moisture; while a drought-resistant species is a species that has special morphological and physiological adaptations to maintain physiological activity, even under conditions of drought stress. A phreatophyte, on the other hand, escapes the drought by gaining access to the water table. All four strategies are represented in savannas, although the drought-enduring succulent is not an important element. The most important strategies are the deep-rooted phreatophyte represented by the majority of savanna trees and shrubs, the drought-enduring perennial graminoids and the drought-escaping strategy represented primarily by a flora of ephemeral annuals. The distinction between drought-enduring and drought-escaping plants is not as clear in savannas as it is in deserts. Each of these adaptive strategies is characterized by well defined phenological, physiological, and morphological characteristics (Sarmiento et al. 1985; Silva 1987; Medina and Silva 1990; Solbrig et al. 1992). The similarity of the adaptive strategies of savanna plants, particularly among the herbaceous stratum, with those of desert plants, indicates probably that there are no unique savanna-adaptive strategies in relation to drought.

Competition for nutrients is also reflected in the characteristics of savanna species. High transpiration rates by the deep-rooted evergreen woody elements even during the dry season, and high root/shoot ratios have been postulated as primarily mechanisms for gathering nutrients (Sarmiento et al. 1985; Medina 1987). It is possible that the relatively large and very coriaceous leaves of many savanna trees represent a unique characteristic related to their nutrient-gathering strategy. This topic is taken up in detail in Chapter 4.

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2.5 Species Diversity, Fire and Herbivory

Plant-available moisture and plant-available nutrients are considered the two principal determinants of savanna function and lead to the concept of the PAM-AN plane, that is theoretically supposed to produce a classification of the world's savannas based upon an ordination of actual sites in relation to these indices. Fire and herbivory were considered to be important in shaping savanna properties at a more local scale (Frost et al. 1986; Medina and Silva 1990; Solbrig 1991a; Teague and Smit 1992).

In relation to both fire and herbivory plant species exhibit two basic adaptive strategies: resistance and escape. Most savanna species are resistant to fire and herbivory and show a series of morphological and phenological traits, such as thick, fire-resistant barks; lignotubers; xerophytic leaves; protected buds; and translocation of nutrients to underground tissues prior to the onset of the dry season when fires occur. These adaptations and the effect of fire on nutrient cycling are well documented (Frost and Robertson 1987). Although fire has probably been present as an important selective factor in tropical savannas for a long time, as attested by the innumerable adaptations of plants to fire, its frequency and intensity has been drastically altered by human presence. Prior to the time when humans started using fire, lightning was the principal source of savanna fires. Some fires are still so started. These fires probably occurred less frequently than fires today, and consequently were of greater intensity. We do not know with precision when humans started using fire as a tool in tropical savannas, but there are remains of hearths as far back as 500 000 years. African savannas have probably been subjected to human-made fires much longer than Australian and American ones, where the human presence is much more recent. No systematic research has been conducted to see whether African species are more resistant to fire than American and Australian ones, but introduced African grasses appear to be more resistant to fire than American species.

There also exists a historical difference between continents in relation to large mammal herbivory. Africa and Asia have had until very recently a widespread and numerous wild fauna of large mammals. Australia never had large herbivorous mammals, and in the Americas the large herbivorous mammals became extinct towards the end of the Pleistocene. It is not known how abundant they were in savanna areas. Cattle was domesticated in the Near East 10 000 years ago and was introduced into African and Asian savannas some 6000 years ago. Its introduction into American and Australian savannas is very recent: in the 16th century in the Americas, only in the 19th in Australia. It is very evident that cattle grazing is a major transforming element in both the American and Australian savannas, and much less so in Africa and Asia. Cattle are also a prime factor in the estab-

ishment of introduced African grass species (aside from the fact that their presence is the result of the importation of these species by the cattle industry). The most plausible explanation for the modifying effect of cattle and the greater resistance shown by African species is selection by large herbivores in the Old World savannas. The importance of herbivory is taken up in Chapter 8.

2.6 Conclusions

The basic question to be addressed by the meeting was developed at an initial IUBS/SCOPE/UNESCO meeting held in Petersham, Mass, in 1991. At that meeting the following null hypothesis was developed: "Removal or additions of species (or functional groups, or structural groups, or ecosystem components) that produce changes in spatial configuration of landscape elements will have no significant effect on ecosystem functional properties over a range of time and space scales" (Solbrig 1991b). In the Brasilia workshop, we circumscribed our discussions primarily to species diversity and functional groups, and explored their effect on resistance and resilience to disturbance, water and nutrient flows, fire, and herbivory.

The null hypothesis refers to the addition and subtraction of species. Addition or removal of species from an ecosystem will change the diversity of the system, both its richness and its evenness (Pielou 1975) and by necessity its function. The question is therefore not whether ecosystem properties are modified when species change, but how and by how much. The objective of this book is to address explicitly the role of species diversity rather than environmental factors in the function of tropical savannas.

In the next chapters we present a discussion on the relations between biodiversity and nutrients; biodiversity and water; the impact of alien invasions on biodiversity of the American savannas; the relation between productivity and diversity; the impact of fire and of herbivores; and biodiversity and stability. We end with a presentation of the discussion held in Brasilia (Chap. 10, 11 and 12) and a general summary (Chapter 13).

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