RESPONSES OF TROPICAL SAVANNAS TO STRESS AND DISTURBANCE: A RESEARCH APPROACH

OTTO T. SOLBRIG, GUILLERMO GOLDSTEIN, ERNESTO MEDINA, GUILLERMO SARMIENTO and JUAN SILVA

Introduction

Tropical savannas are very heterogeneous ecosystems and are consequently hard to define. They comprise a series of ecosystem types which form a distinct biome (Huntley and Walker 1982, Sarmiento 1984). A savanna can be defined as 'an ecosystem of the warm, lowland tropics dominated by a herbaceous cover consisting mostly of bunch grasses and sedges that are more than 30 cm in height at the time of maximum activity, and show a clear seasonality in their development, with a period of low activity related to water stress. The savanna may include woody species (shrubs, trees, palm trees), but they never form a continuous cover that parallels the grassy one' (Sarmiento 1984).

Almost one-fifth on the world's population lives in areas that are presently or were in the recent past covered with savanna vegetation, many of them in rural societies that depend on subsistence agriculture. Per capita food production in these communities is usually low, the result of a variety of environmental, social and economic constraints. Rainfall in these regions is highly seasonal and variable, leading often to uneven and unpredictable patterns of primary production. Many savanna soils are relatively infertile, particularly in the high rainfall zones. This is reflected in low crop yields and in poor nutritional quality of natural pastures, especially during the dry season. Compounding the effects of these factors is the dual nature of land use in many savanna regions. The most productive lands are often set aside for cash crops while the poorer lands are used for local food production or extensive cattle grazing (Kowal and Kassam 1978). Combined with the continuing rapid growth of the human population in the tropics, this pattern of use is placing increasing pressure on marginal lands, resulting in many cases in degraded environments, reduced productivity and low carrying capacity. In order to arrest or reverse these changes we need to acquire a better understanding of savanna dynamics under prevailing and projected patterns of land use, and to find alternative models of development designed to increase the satisfaction of human needs without causing a decline in long term productivity and resilience. To be successful these programs need to be based on scientifically sound technologies which take into account the relevant physical, biological and human elements of the system. Unfortunately, our knowledge of these features, particularly their dynamic aspects, is still quite fragmentary. Over the past few years, research data on savannas in different parts of the world have been synthesized (Hills and Randall 1968, Bourliere and Hadley 1970, UNESCO 1979, Walker 1979, Huntley and Walker 1982, Bourliere 1983, Beck 1983, Sarmiento 1984, Tothill and Mott 1985, Frost *et al.* 1986). These syntheses provide a foundation upon which a comprehensive theory of savanna structure and function can be built.

Seasonal savannas can be managed at least at three contrasting levels of technolo-

gy and production. The first is that of the traditional extensive livestock grazing that does not employ inputs of any kind (fertilizers, pesticides, energy, machinery, improved varieties, etc.). This is the simplest way of utilizing the savanna, the least costly, and the least productive. The other extreme is represented by the replacement of savanna grasses by introduced grasses (or other crops). Without irrigation only one annual crop (*e.g.*, corn, sorghum, cotton) can be obtained in the seasonal savanna. Only through the use of species that are resistant to drought (such as *Punicum maximum* or *Hyparrhenia rufa*) and not too nutrient-demanding, can a permanent artificial grassland be maintained. The investment is relatively high, as is the resultant primary and secondary productivity. Between these two extremes, are systems of medium-intensity management, that involve simple technologies (burning, differential grazing), low levels of inputs (fertilization, some energy), that lead to a notable increase in productivity in comparison with the extensive system.

An international collaborative research program, involving carefully planned comparative studies with a common aim and approach, offers the best opportunity for gaining the insights that are so urgently needed as a basis for the rational use and management of savannas. The International Union of Biological Sciences initiated such a program of research titled 'Responses of Savannas to Stress and Disturbance,' part of the 'Decade of the Tropics,' with the objective to 'develop a predictive understanding of the ways in which savannas respond to natural and man made stresses and disturbances' (Solbrig and Golley 1982, Frost *et al.* 1986).

In this paper, we briefly describe a conceptual model of savanna function and its possible implications for management, which serves as the basis of our research program in Venezuela.

Dynamics of savanna resources and ecosystems processes

Water and nutrients are the basic resources that limit productive processes in savanna. Soil moisture regimes, in turn, are affected by (1) the total amount and seasonal distribution of annual rainfall and the proportion of this water that enters the soil, (2) by the water holding capacity of the soil, which is largely a function of soil particle size and depth, and (3) by the amount of evapotranspiration, which is related in complex ways to climate, soil particle size and surface characteristics, and the type of vegetation at the site.

In order to understand the essential role of water, it is necessary to emphasize that tropical savannas are seasonal systems; that is, their fundamental ecological processes develop in two contrasting rhythms during each annual cycle, passing from a period of intense and diversified activity to one of more or less prolonged low activity of the vegetation. Excepting in areas lying near or within the subtropics, that is, where temperature has a pronounced seasonality, there is no true dormancy among grass species. Mean annual rainfall in savannas ranges from about 300mm to 1600 mm and normally does not exceed potential evapotraspiration, though it may do so seasonally. The American savannas in contrast to the African and Australian tropical ecosystems are exclusively humid (precipitation mostly above 1000 mm)(Sarmiento and Monasterio 1975). This intrinsic seasonality is clearly expressed in the structural and functional changes of the ecosystem throughout the year, and by the rhythmicity of the productive processes (Sarmiento 1984).

The soil-water dynamics in American savannas appears highly correlated with community structure and composition along moisture gradients (Silva 1972, Silva and Sarmiento 1976a, 1976b). The effects of variation in rainfall are compounded by differences in permeability and moisture retention properties among soils. Savanna soils vary widely in particle size, structure, profile and depth, reflecting at one scale the interaction of geology, geomorphology and climate, and at another the influence of topography, relic features of past landforms, the kind and extension of vegetation cover, and animal activity (Young 1976, Montgomery and Askew 1983).

The herbaceous component of the savanna is the controlling element of the system and regulates the fundamental ecological processes such as water balance, productivity, mineral cycling, fires, and herbivory. Although this stratum is referred to as continuous, it only is such at the height of its growth, since the actual basal area of the grasses may only be 10-20%. Although the common species have wide geographical distributions, each species has a definite phenology and microdistribution.

An unmistakable feature of savannas is the coexistence of herbaceous and woody plants in a characteristic pattern where the woody species grow dispersed in a matrix of a more or less continuous layer of herbs, mostly C_4 grasses. This coexistence has been hypothesized (Walter 1969, Walker 1985, Frost *et al.* 1986) to be the result of a partition of the soil substrate into two horizons: a superficial one dominated by the roots of herbaceous plants, and a deep one controlled by the roots of trees. According to this theory, the importance of trees diminishes when the water table is very deep, or when soils become shallow, be it on account of a well developed lateritic hard pan (Santamaria and Bonazzi 1963, 1964, Santamaria 1965), or plintite layer. The first two cases are common in high plateaus, the latter is typical of alluvial plains. In areas with low precipitation, or very good drainage, trees are absent or restricted to depressions where water accumulates (Sarmiento and Monasterio 1971) while in wet areas with poor drainage, trees are found only on elevations. That is, the dynamics of water in the landscape controls the structure of the community at this first physiognomic level.

Nutrient cycling in tropical savannas is only incompletely understood (Medina 1987). Dystrophic savanna soils derived from the weathering of acid crystalline rocks or from ancient sedimentary deposits generally have a low reserve 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 exchangebale bases, particularly Ca and Mg (Jones and Wild 1975, Lopes and Cox 1977, Mott *et al.* 1985). Phosphorus (P) levels are sometimes also very low, and soils rich in sesquioxides have a high capacity for fixing P. Some highly weathered soils also have high levels of exchangeable aluminium (Lopes and Cox 1977).

Three other factors also play an important differentiating role in pedogenesis: topography, parent material, and age. The principal influences that relief has over the ecosystem is on the regulation of the drainage conditions, and ultimately over the water balance. This influence in turn translates into important consequences regarding the chemical and nutritional characteristics of the soils. The factors that produce the relief, through their action on pedogenesis, have indirectly determined the physico-chemical characteristics of the soils (Sarmiento 1984).

The nutrient status of the soil is related principally to the age of sediment deposition. The poorest soils (oxisols and ultisols) are those derived from the oldest deposits, since these materials have been subjected to pedogenic processes for

prolonged periods of time. There exist a large number of studies that contain information on soil nutrient status in American savannas (Zinck and Urriola 1970, Guerrero 1971, Guerrero and Cortes 1976, Leon and Botero 1980, Torres 1980, Sarmiento 1984). These studies agree in classifying the soils of the Venezuelan savannas as oligotrophic, acid, very poor not only in micronutrients but also in many other essential nutrients such as sulphur (Avilan and Rojas 1975, Gualdron and Salinas 1982). Furthermore these soils are high in aluminum (Vargas 1964), considered toxic especially for crops; this topic is controversial (Medina 1978, Sarmiento 1984).

With the exception of extremely acids 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 increased 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 increased belowground production since fire effectively mineralizes most of the aerial matter produced (Sanford 1982, Menault *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; Menault *et al.* 1985). According to these authors, these compounds are produced in inverse proportion to their level in the soil, and consequently earthworms and plant roots are supposed to act as regulators of organic matter decomposition in the soil. Because much of the assimilable carbon required by mineralizing bacteria is apparently confined to root exudates and earthworm casts, nutrient release may be highly localized. It has been observed in African humid savannas (Menault *et al.* 1985) that absorbing roots often tend to follow earthworm galleries where microbial activity and mineralization is very active. An interesting, but as yet unanswered question, is whether different grass species differ in the quantity and quality of root exudates they produce, which could have important ecological implication.

The nutrient dynamics in American savannas is poorly known. Medina (1982) and Sarmiento (1984) have summarized existing knowledge on nutrient partitioning between various compartments in the ecosystem and have proposed preliminary models for the nitrogen cycle and other elements. The principal conclusions of these studies are that fire represents the principal 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 nutrient resources through savanna ecosystems is tighly linked to the flow of water through the soil-plant-atmosphere continuum. Pulses of energy and nutrient input to the biotic components of the ecosystem result from pulses of production by plants, primarily grasses. These latter pulses occur mostly during the wet season, when adequate soil-moisture availability allows transpirational water fluxes from the soil through the plant to the atmosphere. When soil moisture is reduced and not readily available to the plant, stomatal closure, or loss of photosynthetic tissues will reduce the uptake of carbon dioxide.

Estimates of the productivity of tropical savanna grasses were carried out during the International Biological Program (IBP). Most of these studies were made assum-

ing that productivity, the gain of new organic matter by vegetation approximated the measured increase in aboveground (shoot) biomass (Cooper 1975, Garcia Moya *et al*. 1986). However, this assumption has proved to be incorrect and has led to underestimation of true productivity by a factor of two or three (Garcia Moya *et al*. 1986; Sarmiento 1984) due to three reasons: (1) belowground production can be as high or higher than aboveground biomass; (2) the methods used in IBP studies assumed that death of tissue occurs only after the peak of production has been reached; and (3) the researchers did not consider that different species reach their peak of production at different times. Recent studies (Garcia Moya *et al*. 1986) in three tropical grasslands that took into account these considerations have obtained values that are 5 to 10 times higher than the standard IBP methods and approximate the figures for tropical forests.

An accurate appraisal of tropical savanna productivity is essential for understanding the input of organic matter into the ecosystem and the amount of material available for producers and decomposers including those in the soil. Such knowledge is also necessary to understand the potential effect of removal of vegetation as a result of fire and grazing. Furthermore, if these new high values prove accurate, the efficiency of light energy 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.

A number of studies have dealt with the woody elements and their behavior in relation to water. Vareschi (1960) was the first to point out the paradox of the existence of tree species with high transpirational fluxes even during the dry season. Phenological studies (Monasterio 1968, Monasterio and Sarmiento 1976, Sarmiento and Monasterio 1983) indicate that savanna trees reproduce and change their leaves during the dry season. Recently it has been shown that the principal species of trees of the Venezuelan savanna have high values of leaf conductance and low values of hydraulic resistance (Catalan 1983). Sarmiento *et al*. (1985) brought forth the hypothesis that savanna trees are the least seasonal elements of the savanna vegetation and that the high transpirational values throughout the year represent an adaptive strategy that allows them to increase nutrient capture and thereby maintain positive carbon balances throughout the year in an environment that is strongly nutrient limited.

Elements of a working hypothesis

Given the assumption that moisture and nutrient availablity are the major determinants of savanna function (Frost *et al*. 1986) any research program on the functioning of savannas must test the rates of change in savanna species composition and production induced by changes in Plant Available Moisture (PAM) and Plant Available Nutrients (PAN), and the specific adaptations of individual species to water and nutrient stress that result from different fire and cutting regimes. Furthermore, since fire and cattle grazing are the principal management treatments, their effect on soil nutrient status, species composition and productivity must be tested specifically.

A predictive understanding of the ways in which savanna grasses respond to natural stresses and human disturbances should also take into account the existence of the

great diversity in life history characteristics and physiology among savanna grass 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. Other species instead grow more gradually, develop their shoots slowly, and enter into their reproductive phase toward the middle or the end of the rainy season. This temporal displacement in the peaks of growth and reporduction may explain partially 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. Premilinary 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 transpirational rates, have higher water use efficiencies (ratio of carbon assimilation to water loss) and higher turgor pressure than intermediate and late growing species. 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 precocious 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 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 belowground organs. 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 outcompeted when nutrient and water availablity increases.

According to this hypothesis early growing species should be (a) more drought resistant, (b) maintain higher turgor pressures during the dry season, (c) have higher water use efficiencies, (d) allocate a relatively high proportion of photosynthate to belowground organs, and (e) should increase in importance along wet to dry gradients. Also, early growers should increase in importance if management practices tend to reduce soil water availability. They can, therefore, be used as indicator species.

Trees are also an important component of savanna ecosystems. They usually explore deeper soil horizons than grasses and, therefore, in wet savannas are exposed to more uniform water levels. Tree species from different savanna types and different continents seem to have a wide array of morphological and physiological characteristics. At least in many neotropical savannas trees tend to be evergreen, have relatively high root/shoot biomass ratios, and large, highly sclerophyllous leaves. Transpiration rates are generally high even during the dry season and leaf water potentials are maintained above the turgor loss point due to the hydraulic properties of the vascular system. Deciduous trees tend to be prevalent in more fertile soils. It is difficult to

separate attributes that enhance the tree's capacity to withstand water stresss from nutrient stress.

We predict that in wet oligotrophic savannas with water available in the subsoil, evergreen trees with an extensive root system ought to predominate, while in environments with a relatively extended wet season and rich soils, trees with large deciduous leaves and relatively small and superficial root systems should dominate. Finally, in semi-arid savannas, trees with small leaves should be found. In dry sites with a short but very distinct wet season, deciduous trees with small leaves should be favored. If precipitation is more evenly distributed, evergreen, drough resistant woody species should be favored. These stress tolerant trees also should be favored if available soil moisture tends to decrease. They should, however, exhibit low inertia to change if nutrients and water status increase.

Our basic working hypothesis, therefore, is as follows. The wet, oligotrophic, seasonal Venezuelan savannas are characterized by climatic seasonality (Sarmiento 1984), and the rhythm of the wet and dry seasons regulates the rhythm of growth and reproduction of the herbaceous and woody vegetation. But wet and dry seasons are not sharply defined, internally homogeneous intervals of time (not even in terms of rainfall), but are rather yearly oscillations in PAM and PAN that in turn regulate the growth rate, that then will 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 onset of the rainy season is characterized by a period of increasing frequency of rainfall which slowly saturates the upper profiles of the soil. Consequently, any species that is active early in the season will face occasional water stress. On the other hand, the ashes rich in nutrients resulting from the fires that have taken place during the dry season, as well as a relatively large dead underground biomass, mean a relatively good soil nutrient environment. Because the PAM and PAN status is more favorable in the upper layers of the soil, early growing species are expected to have primarily superficial roots. Furthermore, at the beginning of the wet season, following the fires the ground is very open and the light environment very favorable. Consequently we expect early species to be of low stature and globose, *i.e.* of a typical bunch grass shape. By blooming prematurely, seeds of early species can germinate immediately and successful seedlings attain a sufficiently large aerial and underground biomass by the end of the growing season to withstand the ensuing drought.

As the season progresses, PAM in the soil becomes more favorable, but the PAN less so, as more nutrients are removed by the growing vegetation. As more biomass accumulates, the light environment within the canopy also becomes less favorable. Roots of later growing species will, therefore, grow deeper into the soil profile, and aerial biomass higher. Finally, toward the end of the growing season, PAM again deteriorates, but the accumulation of both aerial and underground dead biomass means that PAN either stabilizes or improves. Light environment within the canopy is now very poor as the canopy has attained its maximum size. We expect late species to be more shade tolerant, and to rely extensively on runners as a means of vegetative propagation during the late growing season. If they reproduce by seeds, these must have dormancy to withstand the dry season, since any seedling that germinates late in the season will not attain the minimum size to withstand the dry season before the end of the rainy period. In other words, the changing status of PAM, PAN and light, circumscribe different niche spaces that are utilized by species with different morphologies, physiologies, and life histories.

Savanna management

Management of savannas is concerned principally with manipulating the two principal factors that control the growth of the grasses of seasonal savannas: water and nutrients. Water shortages are seasonal. A season without available soil water for the herbaceous vegetation with more or less shallow roots followed by a wet season. This environmental constraint and the corresponding drought stress it induces on savanna grasses are very hard to correct. If possibility for irrigation exists, it cannot be justified economically to maintain a natural grassland, since irrigation offers more lucrative alternatives: improved grasslands or crops.

Nutrient availability can, however, be modified combining low levels of fertilization with simple and not too expensive management techniques such as the regulation of fire and grazing. This can improve the nutrient status of the soil through an acceleration of natural nutrient cycles, an increase in the nutrient stock, and a reduction of nutrient losses.

There is little information on the effects of fire on the population dynamics of savanna species. Fires may affect populations by (1) killing seeds; (2) promoting germination of seeds; (3) damaging seedlings, thereby, retarding their growth and jeopardizing their survival; (4) killing seedlings outright; (5) damaging adult plants through destruction of leaves, shoots, meristems, or flowers, that may lead to slowing down growth and even eventual death of plants; (6) promoting growth of burned plants; and (7) by affecting flowering probabilities (either by promoting or hindering flowering). The effect of fire may be direct as a result of burning, or indirect by changing water and nutrient supplies. It is important that we learn how fire affects the population and which life history traits are most affected. Only in this way can fire be used as a management tool to promote desirable effects and avoid undesirable ones. On the basis of our experience, we can make the following predictions which we hope to test experimentally.

We expect that fires during the dry season will kill a fraction of the seeds in the soil. This should impact, especially, population growth of species that rely mostly on seeds for reproduction and have a relatively short life cycle, and least those species that are characterized by long life cycles, low turnover rates and a high rate of vegetative reproduction. Dry season fires should not have a great effect on the seeds of early and precocious species, since their seeds germinate as soon as they are dispersed.

Fire should have a damaging effect on seedlings if it occurs during the critical first months of growth, before there has been time to develop the first rhizome. Survival will be greater the deeper the seedling's meristems are buried in the soil. The precocious species bury their meristems deeper than the other groups. Late blooming species usually have their meristems above the ground, at least during the critical early months. Consequently, recruitment of short lived species will be most affected by dry season fires both on account of their morphology and their high dependence on seedling recruitment.

Fire will also have a differential effect on adults of savanna species, sometimes even within a particular type, based on the position of the rhizomes and meristems. So, *Leptocoryphium lanatum* has its rhizomes five or more cm below ground (sometimes as deep as 20 cm), while other species of this type have them between 2-5 cm below ground. This difference may not be important since the soil temperature is not affected by fires. Furthermore, most savanna species build mounds around their

base, that protect their meristems from burning. There are exceptions, however. Working with *Sporobolus cubensis*, Silva (1987) found important negative effects of late dry season fires on vegetative growth of adult plants. He documented a decrease in the rate of shoot production during the growing season compared to unburned controls.

Fire should have a greater negative effect if it occurs during the time plants are physiologically active. Consequently late dry season or early wet season fires should affect precocious and early growing species more than other types. However, the effect of fire is more complicated, since different events interact in population dynamics. Increased mortality of adult individuals may affect less species of short life cycles because of their rapid recovery through seedlings. This implies that fire affects seedlings and adults differently. If both are affected equally, then species with long life cycles and high rates of vegetative multiplication should increase in abundance. By carefully monitoring the growth and survivorship of seedlings and adults of a number of these species and of the very successful introduced African grass *Hyparhenia rufa*, we hope to be able to develop more precise models to predict the effect of fire on species composition of the savanna.

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