In: Pereira, R.C., Nasser L.C.B. (eds). 1996. Biodiversity and Sustainable Production of Food and Fibers in the Tropical Savannas, EMBRAPA, Brazil, pp. 6-9.

FIRE AS A FACTOR INFLUENCING THE DIVERSITY OF LIFE FORMS IN NEOTROPICAL SAVANNAS

JUAN F. SILVA
Centro de lnvestigaciones Ecologicas de los Andes Tropicales, Fac. de Ciencias. Universidad de Los Andes (ULA), Mërida, Venezuela.

LIFE FORMS

Life forms, growth forms, architectural models and biomass allocation patterns are different names given to the study of the diversity of plant growth. Although life form analysis is a promising approach since it encompass ecological and evolutionary basis for the study of plant morphology, it has developed very little since the Raunkier’s life form system. Since morphology is closely related to function, the life form approach is essentially dynamic and based on a morpho-functional view of plant diversity. Raunkier’s system has this morpho-functional view since the position of buds relates to survival mechanisms, architectural designs and the dynamics of seasonal regrowth. However, it was designed for temperate communities and is of very limited use in tropical terrestrial ecosystems. There is a need to develop ecologically sound systems for the analysis of life form diversity in tropical vegetation.

Beyond the description of growth forms of savanna plants, little have been done to develop comparative systems to allow the study of life form diversity and the factors influencing it. Several difficulties have to be overcome in order to develop such a system. Several species are not easy to classify because their growth habit is a partial response to seasonal drought and fire. Many of both herbaceous and woody species rely on seasonal regrowth from underground meristems, but there is little detailed knowledge about underground plant architecture. Furthermore, functional properties of savanna plants are still largely unknown.

The functional significance of life forms is relevant for the sustainability of the savanna ecosystem and for the study of the evolution of the savanna plant biota. Functional aspects include phenological, demographic and physiological properties of plant species that are pertinent in terms of individual survival and reproduction. However, each of these aspects is rich in many functional details and we risk to be carried away with the impressive array of variations and combinations that may entangle the comparative approach.

Sarmiento & Monasterio (1983), based on a phenological approach, classified savanna plants in three large groups: a) annuals, b) with seasonal above ground parts and c) with perennial above ground parts. The first group is small and variable according to the habitat. In the other two groups there is a wide variety of morpho-functional types, which are described by these authors. Group (b) contains two subgroups: plants with woody underground organs and with herbaceous underground rhizomes. The approach taken by Sarmiento and Monasterio combines two very important qualities: it is simple and it is meaningful. A system based on three main groups with few subgroups encompass most of the morpho-functional diversity of tropical savannas. It also allows to consider effects of environmental factors in the short-term (ecological) scale and the long-term (evolutionary) scale. However, two aspects of this system deserve further discussion: a) subgroups are still to be defined; and b) their functional differences need to be clarified.

The principle of parsimony should be kept in mind to develop the Sarmiento-Monasterio system keeping intact its powerful simplicity. To elaborate in this direction, a preliminary classification is intended in the diagram showed in Figure 1. We made some additions to the four original terminal groups by differentiating between deciduous and evergreen in the group with perennial above-ground biomass. We also separated the group with fleshy underground perennating structures into graminoids and broad-leaved plants. Observe that in this classification the first two hierarchy levels are functional: level I based on demographic properties and level II based on phenological properties.

Concerning functional roles, it seems now clear that evergreen neotropical savanna trees are functionally different from and complementary with the concurrent graminoid species (Goldstein & Sarmiento, 1987; Solbrig eta!., l995b). This is concerned with water, carbon and nutrient cycles and the plant responses to the seasonality of energy, water and fire regimes. Functional differences between those two life forms and the half-woody forms are still unclear. Differences concerning nutrient supply (Medina & Huber, 1992) seem to be important between grasses (more dependent on nitrogen supplj) and legumes (more limited by phosphorus supply), and these may be related to the distinction between graminoids, broad-leaved herbs and subshrubs. Functional differences between evergreen and deciduous savanna trees are still unclear, although differences in carbon balance have been related to their contrasting biomass allocation patterns (Azócar *et a!.*, 1996).

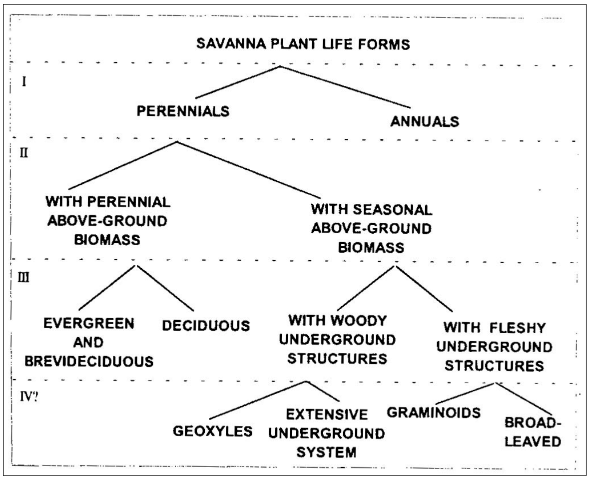

FIG. 1- The Sarmiento-Monasterio system of savanna life forms showing four hierarchy levels with seven terminal life forms. Categories at level IV are tentatively suggested in this paper. Further divisions of evergreen and deciduous perennials as well as of annual plants and graminoids could be included. (Diagram based on Sarmiento & Monasterio, 1983).

FIRE AS AN ECOLOGICAL DETERMINANT

The two most important environmental factors determining the diversity of savanna ecosystems in the neotropics are water and fire as already stated by Warming (1892). According to soil texture and depth, availability of moisture for plant growth is well stratified in the soil profile, and it follows an annual rhythm according with the seasonality of rainfall (Medina & Silva, 1990). It is also affected by annual fluctuations in total amount of rainfall, resulting in sequences of drier or wetter years, although this has not been well documented. On the other hand, fire is an episodic event whose frequency has increased with human settlements. The effects of savanna burning depend largely on the frequency and intensity of fire, and these depend on the annual production of the grass layer which in turn is a function of annual rainfall. Fire and water are therefore interacting determinants (Silva, 1995).

Fire, usually taking place at the end of the ‘dry season, causes different and sometimes opposing effects. It kills, not only woody plants but also dominant graminoids (Silva *et* a!.. 1990,1991). It suddenly changes the amount of radiation. and hence the temperature, at the soil surface and releases mineral nutrients trapped in the standing biomass. Fire stimulates the germination of some species, the regrowth of the aerial biomass and the flowering of herbaceous species (Frost & Robertson, 1987). The synchrony of burning with the onset of rains reinforces the seasonal rhythm of savannas, producing a burst of energy, water and nutrients at the soil surface where the buds of most savanna species are then in a dormant condition (Solbrig et al., l995a).

FIRE AS A SELECTIVE FORCE

Savanna fire regime is influencing plant and population growth in the short ecological term and it seems to be an evolutionary force shaping plant form and function in tropical savannas. In their remarkable 1983's paper, Sarmiento & Monasterio analyzed many examples of the plastic responses of different woody life forms to fire regime and forwarded several interesting hypotheses on the evolution of adaptive responses to fire in several groups of woody species. Savanna woody species show an extraordinary plastic versatility, partially due to their special meristematic arrangement. This increases survival to burning and is considered an important factor for savanna stability (Archer *et a!.,* 1995**).**

Fire regime may also be acting as a selective force shaping savanna grasses. Some grass species have to rely on underground reserves in order to rapidly regrowth their foliage and bloom after savanna burning. In contrast to other grasses, they show high rates of below/above-ground biomass allocation patterns (Silva, 1987). These architectural and phenological patterns are concurrent with other life history traits, suggesting adaptive arrays (Sarmiento, 1992). Furthermore, annual and perennial grasses differ in their ability for population survival under different fire regimes (Canales *et al.,* 1994; Silva, 1995; Silva *et a!.,* 1990, 1991). Some species may have evolved from tolerance to dependence on high fire frequency because of human induced burning of savanna vegetation (Silva *et al.,* 1991).

Several traits (such as underground reserves of water, energy and meristems) which increase survival during dry spells also decrease mortality from fire. During dry years fire is less likely to occur, but during wet years, the probability of fire occurrence and fire intensity increase. This is the reason fire and water availability seem to be acting in complementary or interacting ways to shape the diversity of life forms in savanna communities.

FIRE AND THE DIVERSITY OF LIFE FORMS

How can we compare savanna communities on the basis of their life form diversity? First of all, we need a classificatory system of life forms more adequate than the Raunkier's system. It seems apparent that general systems for the world's vegetation are unlikely to be successful. Classificatory systems for specific types of communities, such as the one suggested by Sarmiento & Monasterio (1983) for neotropical savannas, may overcome the shortcomings of wider approaches. Furthermore, we need suitable indexes to measure life form diversity. Commonly used indexes to measure the diversity of species in a community are perfectly adequate for this purpose. In this way, we take into account the number of life forms present in the community (richness) and how these life forms are represented in the community (relative number of species in each life form).

Sarmiento (1983) analyzed species and phenological diversity of the grass component along moisture gradients in Venezuelan savannas with the same index. A more recent attempt to measure species and functional diversity to compare different savanna communities in western Venezuela showed a strikingly similar pattern of variation of both diversities (Castillo, 1995). In this study, ten different functional groups were used. Unfortunately, none of these two studies have to do with the influence of fire regime.

We expect the relationship between diversity of life forms and fire frequency in savannas to be bell-shaped (Fig. 2). This type of response to frequency of disturbance has been found in different communities, although not for the same causes (Fuentes, 1988). Some life forms, such as deciduous trees, are more susceptible to mortality by fire than others. As the frequency of fire increases, density of deciduous trees decreases because the likelihood of individuals being killed becomes higher, even within the small forest islands. Evergreen trees have higher probabilities of survival to fire than deciduous trees, and that is the reason they grow isolated in the grassland of frequently burnt savannas. However, even they can be importantly reduced as fire frequency increases, as suggests the increase in their density after several years of fire exclusion (San José & Fariflas, 1991). Similar consequences are expected for the broad-leaved herbaceous species. In summary, after a certain threshold of increased fire frequency, the savanna would be reduced to an almost pure grassland. On the other hand, it has been shown that some savanna grass species are unable to persist below certain rather high fire frequencies (Canales *eta!.,* 1994, Silva *eta!.,* 1991). This is due to the reduced light incidence at the ground level, not because of the competitive effects of tree cover but rather because of the increased accumulation of standing nechromass after several years without burning. This may affect other life forms depending on regrowth from underneath the soil, such as the hemixyles.

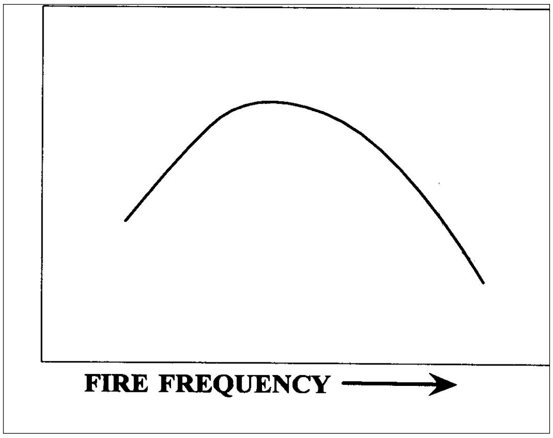

FIG. 2- Predicted variation of the diversity of life forms in savanna communities as a function of the frequency of fire. Diversity decreases as a consequence of the increased probability of death as follows: a) on the right hand, due to burning in those species which are less able to cope with fire; b) on the left hand, due to shading in those species which are unable to tolerate the shade from accumulated standing nechromass but have to regrow from soil surface.

REFERENCES

ARCHER S. COUGHENOUR, M.; DALL'AGLIO, C.; FERNANDEZ G.W; HAY, J.; HOFFMAN, W.; KLINK, C.A.; SILVA, J.F.; SOLBRIG, O.T. , Savanna Biodiversity and Ecosystem Properties. In: SOLBRIG, O.T., MEDINA, E. SILVA, J.E, eds. Biodiversity and Savanna Ecosystem Properties. Berlin: Springer-Verlag 1996. pp. 207-218.

AZOCAR, A; RADA, F. SILVA, J.F Gas exchange and carbon balance in deciduous and evergreen trees from venezuelan savannas. (submitted) 1996.

CANALES, J; TREVISAN, M.C., SILVA, J.F; CASWELL, H.A. demographic study of an annual grass (Andropogon brevifolius Schwarz) in burnt and unburnt savanna. Acta Oecologica, v. 15, : 261-273, 1994.

CASTILLO, A. Funcionamiento y diversidad de ecosistemas de sabanas en los Llanos Occidentales de Venezuela, Estado Barinas. Mérida, Venezuela: Facultad de Ciencias, Universidad de Los Andes, 1995. Tesis de Maestria en Ecologia Tropical.

FROST, P.G.H.; ROBERTSON, F. The ecological effects of fire in savannas. In: WALKER, B.H., ed., Determinants of tropical Savannas, Paris: IUBS, 1987. p. 93-140

FUENTES, E.R. The hump-backed species diversity curve: why has it not been found among land animals? Oikos,
v.53,p.139-143, 1988.

GOLDSTEIN, G.; SARMIENTO, G. Water relations of trees and grasses and their consequences on the structure of savanna vegetation. In: WALKER; B.H, (ed) Determinants of tropical Savannas, Paris: IUBS, 1987. p.13-38.

MEDINA, F.; HUBER, O. The role of biodiversity in the functioning of savanna ecosystems. In: SOLBRIG, O.T. van EMDEN, H.M.; van OORDT, P.G.W.J., eds., Biodiversity and global change, Paris: IUBS, 1992. p.
139-158.

MEDINA, F.; SILVA, J.F. The savannas of northern South America: a steady state regulated by water-fire interactions on a background of low nutrient availability. Journal of Biogeography, v.17, p. 403-413, 1990.

SAN JOSE, J.J.; FARIÑAS, MR. Temporal changes in the structure of a Trachypogon savanna protected for 25 years. Acta Oecologica, v.12, p.237-247, 1991.

SARMIENTO, G.; MONASTERIO, M. Life forms and phenology. In: BOURLIERE, F. ed., Tropical Savanna. Amsterdam: Elsevier 1983. p. 79-108.

SARMIENTO, G. Patterns of specific and phenological diversity in the grass community of the venezuelan tropical savannas. Journal of Biogeography, v.10, p.3713-391, 1983.

SARMIENTO, G. Adaptive strategies of perennial grasses in South American savannas. Journal of Vegetation Science, v.3, p.325-33^6, 1992.

SJLVA, J.F. Responses of savannas to stress and disturbance: species dynamics. In: WALKER, B.H. ed., Determinants of tropical savannas, Paris: IUBS, 1987. p. 141-156

SILVA, J.F. Biodiversity and stability in tropical savannas. *In:* SOLBRIG O.T., MEDINA, F. SILVA, IF. eds., Biodiversity and savanna ecosystem processes., Berlin: Springer-Verlag, 1995. (in press).

SILVA, J.F; RAVENTOS, 1.; CASWELL, H. Fire, fire exclusion and seasonal effects on the growth and survival of two savanna grasses. Acta Oecologica, v.11, p.7 83-800, 1990.

SILVA, J.F.; RAVENTOS, J.; CASWELL, H. Population responses to fire in a tropical savanna grass: a matrix model approach. Journal of Ecology, v.79, p.345-356, 1991.

SOLBRIG, O.T.; MEDINA, E.; SILVA, J.F. Biodiversity and tropical savanna properties: a global view. *In:* Mooney H.A., J.H. Cushman, E. Medina, O.E. Sala and E.D. Schulze (editors), *Biodiversity and global change*. SCOPE 55, J.Wiley. p. 185-205.

SOLBRIG, O.T.; MEDINA, E.; SILVA, J.F. Determinants of Tropical Savannas. *In:* SOLBRIG O.T., MEDINA, E.; & J. SILVA, J.F., eds., Biodiversity and savanna ecosystem processes., Berlin: Springer-Verlag. P. 31-44. 1996.

WARMING, E. Lagoa Santa: contribuçâo para a geographia phytobiologica. Belo Horizonte: Editora Itatiaia,. 1973. 282 p.