1. INTRODUCTION

The weight of evidence related to changes in savanna community composition concerns changes in the prevailing pattern of events such as fires, grazing and rainfall, as well as changes in the nutritive status of the soil. However, we know very little about the processes which are involved in these changes. Sound management practices require not only a basic knowledge of the processes taking place in a savanna community reacting to an environmental change, but also a theory as to why these processes occur (Jones & Mott, 1980).

We are primarily concerned with changes in community structure. The structure of a savanna community could be considered in different ways: trees vs herbaceous species, palatable vs unpalatable species, etc. In its most general form it is the species composition and the relative importance of each species present in the community. Changes in community structure, therefore, are changes in the species composition and their relative abundances. In some cases the standing biomass is made up of only a few species, with many minor species. This balance may change from one site to another, but what is important is that the community has the potential to change in its structure in response to a change in the prevailing environmental patterns. Thus, no matter how low the relative importance of a species might be at any one time, it is an essential component of the potential of the community to change.

Since community changes imply population processes, we require information on the key aspects of life history and population susceptibility to environmental changes. There are a series of important parameters to be considered, such as longevity, reproductive effort, annual reproductive output, vegetative vs. seed reproduction, seed dynamics and germination, mortality factors, phenology, growth forms, etc. Because savannas are very diverse communities and they differ widely in floristic composition throughout the world, we face the long task of characterizing their different population dynamics and their reactions to environmental changes. I believe that this can be solved if we find patterns of responses to changes based upon the interactive nature of life history traits. In this
paper I will discuss some possible ways of detecting these patterns.

Let us consider the following questions:

1) How different are coexisting species in their life table characteristics?
2) What is the role of these differences in the response of the populations to disturbance or environmental changes?
3) How are these responses related to community changes?
4) What types of interactions between species are involved in their demographic responses to disturbance or environmental changes?

2. THE TIME OF ANNUAL REPRODUCTION

From a population point of view, the time of flowering and seed dispersal is important, particularly in seasonal environments such as savannas. Flowering and fruiting represent important energy investments and are essential to population persistence. An example of the reproductive phenological pattern in savannas is given in Fig. 6.1. It is the pattern observed in the Orinoco Savannas. This phenological diversity, studied by Monasterio & Sarmiento (1976) and Sarmiento & Monasterio (1983) shows the phenological spread between codominant grass species. Some species flower by the end of the dry season and beginning of the rainy season and grow rapidly (Sporobolus cubensis, Brachypodium lanatum) whereas others grow more slowly and flower around the mid- rainy season (Axonopus canescens, Trachypogon plumosus). Still others grow even later and flower only at the end of the rainy season (Andropogon semibicolor).

Consider a precocious flowering grass species (A) and another grass species (B) which flowers late in the rainy season (Fig. 6.2). Both rely totally on seed reproduction for population maintenance. By the end of the dry season most of the above ground biomass is dry, species A starts to grow as soon as the rains start, producing new leaves and flowering, while species B only grows vegetatively. As growth proceeds, above ground biomass becomes less and less palatable, since its protein: fibre ratio decreases. By the end of the rainy season, the late species (B) flowers. Flowering is in both cases essential for population growth, since the amount of flowers determines the amount of seeds.

This difference in time of flowering is not the only difference between precocious and late species. Precocious species have their peak of growth earlier in the rainy season, and the difference between the two is represented in the figures by the boxes.
This difference may be very significant in terms of relative changes in population sizes when considering changes in the environment. If this savanna is burned by the end of the dry season, several things may happen.

As Coutinho (1976, 1982) has shown, late-dry season fires stimulate the flowering of precocious species. This implies that under this fire regime, precocious species increase their annual reproductive output (Fig. 6.2, F1) and the population should grow. Working with Sporobolus cubensis, a precocious species from seasonal savannas, we found that fires not only increase the flowering but also reduce vegetative vigor and size of adult plants (Canales & Silva, 1986). On this basis we would expect that S. cubensis in a community with late-dry season fires would have less vegetative vigor and higher annual reproductive investment than in protected savannas. In population terms this implies displacement towards faster turnover rates, i.e. towards the "F" type strategy.

Late-dry season fires do not seem to have much effect upon late species, not only because their growth is still slow, but also because their reproductive activity is not evident.
If we consider grazing pressures, the precocious populations will suffer more because the new growth, with higher proportion of protein and therefore more palatable, includes the flowers. Thus, much of the reproductive effort of precocious species would be lost to grazing (Fig. 6.2, G). Later species are much less affected. By burning the dry biomass, fire makes new growth more accessible, and grazing pressure becomes more important. Reproductive losses by precocious species will be higher.
If we consider mid-rain season fires, then the situation would be reversed. Late species would lose all the energy invested in new green biomass and their inflorescences or the developing floral stems, and therefore will not produce seeds that year (Fig. 6.2, F2-1). Precocious species may not be affected as much since their flowering has passed. Moreover, we know that some precocious species flower after any fire, increasing the annual seed crop (Fig. 6.2, F2+). Timing of reproduction is indeed very important, in terms of the species responses to changes in fire and grazing regimes. We can speculate on the evolutionary consequences of these pressures. If precocious species are indeed palatable, they could not survive. Thus, we would predict that the leaves of precocious species are less palatable than the leaves of late species.

3. PHENOLOGY, GROWTH FORM AND DEMOGRAPHY

In order to detect patterns of responses to environmental changes it is important to determine how, in a functional manner, the different aspects of the species life histories are related. In a study of coexisting grass species in a savanna community from western Venezuela (Silva, 1983; Silva & Altaroff, 1985) we found several important relationships between phenology, growth forms and population parameters. Fig. 6.3 presents a brief summary of the most important traits of the six grass species mentioned earlier.

The three phenological groups differ clearly in growth forms and below-above ground biomass ratios (B/A). The precocious are bunch grasses with high B/A, the intermediate could be considered low tall-grasses since they grow leafy culms but show intermediate B/A and the late species is a true tall grass with a very low B/A. These correlated differences may be very important, particularly since fire and grazing remove the above ground biomass. The proportion of energy reserved in the rhizome should be much higher in precocious than in late species.

In intermediate and late species the seeds produced lay dormant in the soil until the following year’s rains, whereas all precocious species seeds germinate as soon as they reach the wet soil. Also, because the former are produced during the peak development of the insect community, they are heavily predated, whereas seed mortality in precocious species is low. The species also differ in annual reproduction rates, with precocious species producing fewer seeds per plant than intermediate and late species.
7. plumosus, however, is an exception. It is the only one with important vegetative spread, and produces as few seeds as the precocious species. When the proportion of total biomass annually invested in seed production is considered, there is no apparent relation to the phenological and growth forms groups, although A. semibarbata invests one order of magnitude higher than the rest.

Since bunch and tall grasses coexist in other savanna communities, these patterns are expected to hold and, as shown with the time of reproduction, they may be functionally important in regard to the species responses to environmental changes.

4. SEED VS VEGETATIVE REPRODUCTION

Populations are made not only of adults but also of seeds, seedlings and juvenile plants. In perennial species all of these stages coexist, and to have a reproducing adult there has to be a surviving seedling which in turn comes from the surviving seed. The important difference comes from the turnover rates of different populations. Some species are short lived and their annual seed crop is higher than in species whose individuals are long living. In the case of grasses, the long lived species show important vegetative spread and very few seedlings are found. In the example given above, A. semibarbata represents the first group and A. plumosus the second (see Fig. 6.3).

In the short term any environmental change negatively affecting seed and/or seedling survival will, clearly, impair a species relying on seeds but have little effect upon a vegetative species. The seeds of intermediate and late species remain dormant on the soil for several months, including the dry season. If a fire occurs many seeds on the soil surface will be killed. This will affect A. semibarbata and A. canescens populations more directly than A. plumosus populations. The populations may react even more differently if we consider disperse structures and their possible role in protection from fire.

Similarly, we could consider the effect of fire on seedling survivorship. Using cohorts of seedlings the role of late- dry season fires were evaluated as mortality factors in the population of the late- flowering species A. semibarbata (Silva & Castro, in preparation). Fig. 6-4 shows the survivorship curve for the first two years. Mortality during the first two rainy seasons is low (22-24%). But, in the first dry season it was very high (84%). During the first part of the dry season (January, February), the slope of survivorship was the same as that during the last part of
the growth season, and relative mortality rate was only slightly higher than in the rainy season (29%). But the occurrence of fire by the end of February brought about a mortality of 74%.

By evaluating fire damage on monitored seedlings, and by setting up experimental plots, the role of late-dry season fires were confirmed as an important mortality factor of *A. cordifolia* seedlings (Silva & Castro, in preparation). It was found that 90% of the individuals surviving drought were killed by fire. The negative effect of fire may be related to growth form, since this species has very superficial, short rhizomes and a very low...
below: above ground biomass ratio. The situation may be different in species such as *L. lanatum* which buries its meristems deep in the soil, and it is probably not important in *Trachypogon plumosus* which shows extensive vegetative multiplication.

It is generally believed that fire confers an advantage on grasses because it is a mortality factor of tree seedlings and saplings. These results show that fire also has negative effects on seedling survival in grasses, and the magnitude of the effects upon the populations depends on the extent to which they rely on seed reproduction.

Our knowledge of different responses to fire and their relation to growth form, phenology and life tables of the species would enable us to develop predictive models of community changes in response to changes in the patterns of fire. As a working hypothesis it would propose: fire affects grass species in different ways and in different stages of their life cycle depending on the time and...
frequency of fire, and on the phenology, demography and growth form characteristics of the species.

5. WATER STRESS AND SEASONAL RAINFALL PATTERNS

Species differing in their phenological behaviour may react differently to changes in seasonal rainfall patterns. Effective rainfall changes not only as a consequence of certain management practices but also due to changes in climatic trends which may reduce the length of the rainy season and the total amount of annual rainfall. These parameters also change spatially, and differences in rainfall patterns and soil characteristics may explain differences in community diversity, i.e. why some savannas have only one of two very dominant grasses and others may have a dozen or more important grass species.

Sarmiento (1983) studied species and phenological diversity in seasonal savannas from Venezuela, and found that most communities have a mixture of phenological types. Cases with only two phenological types were rare. He discussed the behaviour of each phenological group in relation to water availability during the growing season on the basis of frequencies of each group and rainfall patterns and soil depth and concluded that each phenological behaviour seems to have its own optimum in the environmental mosaic, as summarized in Table 6.1. The results were explained in terms of physiological adaptations to water use, but the table also demonstrated that the preference of each group is related to water availability for the critical period of flowering and seed set.

<table>
<thead>
<tr>
<th>Soils</th>
<th>Climate</th>
<th>Relatively moist</th>
<th>Relatively dry</th>
<th>Short rainy season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shallow</td>
<td>(May to Nov) Late</td>
<td>(From May - Intermediate)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deep</td>
<td>(Apr to Oct) Precoceous</td>
<td>(May to Oct) Early</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 6.1. Some relationships between climate, soils and frequency of phenological groups of perennial grasses. (From Sarmiento, 1983).
A change which decreases water availability during April will have negative effects on precocious species since seed production will decrease, but it will not affect seed production in the other populations. A decrease towards the end of the rainy season will have a greater affect on the late species. A decrease in rainfall during the mid-season months will affect the intermediate species, which seem to be drought-avoiding species, more than the rest. We do not know precisely how changes in total rainfall relate to the patterns of monthly rainfall, but it seems that a decrease in annual precipitation affects the transitional months (April and November) more than the May to October season. If so, then precocious and late flowers will be negatively affected by a reduction in total annual rainfall.

As a further working hypothesis, it is proposed that if changes in total annual rainfall and effective rainfall affect the temporal patterns of water availability in the soil, they will also differentially affect the reproductive output of species depending on their reproductive phenology and the extent to which they rely on seed reproduction. This will consequently result in changes in community structure.

6. INTERACTIONS BETWEEN SPECIES

Changes in prevailing environmental patterns affect different species in different ways. To this direct effect we must add indirect effects: changes in one population will surely affect other species populations with which it interacts. The importance of these indirect effects depends on the magnitude of the interactions. For instance, competitive interactions between species means that the direct effect of grazing on the size and relative importance of one species generates an indirect effect of increasing a competitor species. This simple view may become more complex if we consider interactions between a large number of species.

Competitive interactions are likely to be more important between closely related species having similar requirements. Also, we have to consider that not only adult plants are subject to competition and that these interactions may exist between different life stages of populations within species.

Very little is known about competitive interactions among savanna species, and what is known is restricted to the woody vs herbaceous components (Walker, 1969; Walker & Noy-Meir, 1982; Kooij & Walker, 1985). In the search for species patterns, the following questions are relevant.
How strong is competition between similar species? Are differences in phenology and growth forms related to temporal and/or spatial partitioning of limiting resources? How do changes in one species population affect other populations?

Differences in phenological behaviour may be related to temporal niche separation in the sense that each species uses limiting resources such as nutrients more intensively at different times during the growing season. It follows that competition between phenologically similar species must be more intense than between species from different phenological groups. Consequently, changes in a given population in response to environmental changes or disturbances will have little effect upon populations of different phenological groups.

By the same token, similar growth forms should compete more intensively for certain resources, like light, than species with very different growth forms. We would then predict that two bunch grass species will show stronger competitive interactions than a bunch grass and a tall grass species. Because close relationships exist between growth forms and phenological behaviour, the prediction is reinforced. Temporal and spatial partitioning should decrease the intensity of competition between otherwise similar species (i.e. grasses).

Competitive interactions between grass species in a seasonal savanna are being studied in order to learn to what extent species competition is correlated to similarities in phenology and growth habit (Raven toes Silva, 1986). The two precious bunch grasses Elyonurus adustus and Leptochloa lanata, and a large species Andropogon semibarbatus were included in a series of growth experiments in one, two and three species mixtures, in the savanna. Some of these results are shown in Fig. 6.5. When growing alone, both E. adustus and L. lanatum reached higher values of cover than when growing in the company of either one or both of the two other species. A. semibarbatus however, was little affected by its companion species.

The depressing effect of each species on the other two was calculated when growing in mixtures, compared to the growth of single individuals (Fig. 6.6). The values, which are an index of competitive interference between species, are strongly asymmetric. There are strong competitive interactions between species, but the original hypothesis does not follow. A. semibarbatus strongly affects the growth of the two precious species, and although the effect of
Fig. 6.5. Changes in plant cover measured throughout the year in three species, growing alone or in mixtures and in some species mixtures.

*Erythroxylum SIMULIO* 1 4 *Ricinocarpus Zonata* 2 *Cocculus Indigos* 3 4 5

Changes in species cover are expressed in player 4 values and 10% to grid

*Species* by *J. Silva, 1992.*
L. lanatum on this late species is rather low (0.11) the effect of E. adustus is high enough (0.44) and similar to the values between the two precocious species (0.57 and 0.42). Therefore, we would expect changes in A. semiberbis to have a strong effect on L. lanatum but not vice versa.

A further point is that in mixtures of three species, the combined effects of E. adustus and A. semiberbis were much higher than the individual effects of these species upon L. lanatum. But, the effects of two species, when one of them was L. lanatum upon a third species was not higher than the major effect of one species alone, and furthermore, the combined effect on A. semiberbis was much decreased. This suggests that the interactions among these species are not just simply negative effects. It is also important to determine if these patterns of interactions among adult individuals apply equally to other life cycle stages. It is well known that seeds and seedlings are the bottlenecks of plant populations dynamics. It is also known for several species that seedling survivorship is strongly correlated with size (Solbrig, 1987; Solbrig et al., 1980). In a demographic study of Andropogon semiberbis (Silva & Castro, in preparation) size was found to be correlated with survivorship both for the rainy and the dry seasons. The effect of adult individuals of several species upon growth of A. semiberbis seedlings was therefore investigated.
The results showed that the effect of competitive interference from adult plants of the three species mentioned above is very high and similar, and that it decreases with distance. Therefore, although adult plants of *L. lanatus* have little impact upon the growth of adult plants of *A. semibarbata*, they have an important effect upon seedlings of this species. Since populations are built up and maintained by the constant flow from seedlings to adults, we cannot ignore interactions between different life stages. Due to rather low seedling densities in the field it seems probable that seedling survivorship does not depend on seedling density.

7. CONCLUSIONS

1) In order to understand the processes and mechanisms involved in savanna community changes in relation to environmental changes, it is necessary to know the main life history traits of the species. This knowledge is still very scanty.

2) The dynamics of a species are affected by environmental changes in two ways: directly, by influencing one or more life stages in the population, and indirectly, by affecting other species, with which this species has strong interactions.

3) The effects of fire, grazing and changes in effective rainfall, upon species dynamics depend on the life history traits of the species of particular importance in this regard are time of reproduction, growth rhythms, seed vs vegetative reproduction and growth forms.

4) There seems to be a close functional relation between phenological, architectural and demographic properties of the populations. Learning the nature of these relationships allows us to detect patterns of species reactions to environmental changes.

5) Relating these patterns to physiological responses of individual plants will allow us to build dynamic and predictive models on the responses of savannas to changes in prevailing environmental patterns. These models are important for the design of sound management practices. The use of fire, already generalised as a management tool, could be much improved in attempts to change community composition in desired ways.


