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CHAPTER 6 - DYNAMICS
RESPONSES OF SAVANNAS TO STRESS AND DISTURBANCE:
SPECIES DYNAMICS
J.F. Silva

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 populational 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, Elyonurus adustus and Leptocoryphium 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 semiberbis).

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.
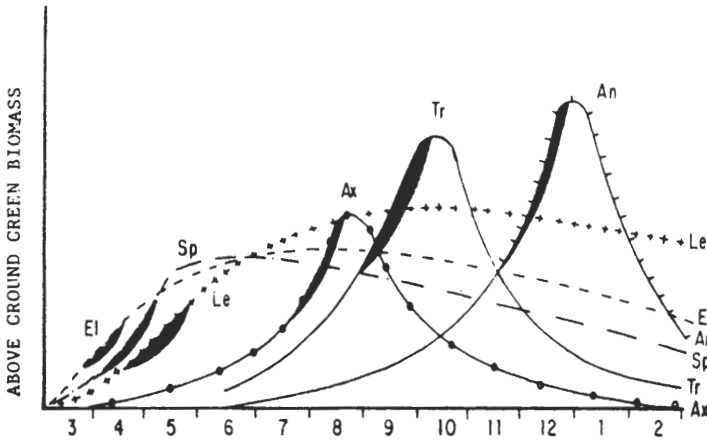
Fig. 6.1.   *Phenological spread between codominant grass
species from a savanna community in Barinas,
Venezuela. Fires occur before April (4) and
are followed by the starting rains, which last
until December (12). El = Elyonurus adustus;
Sp = Sporobolus cubensis; Le = Leptocoryphium
lanatum; Ax = Axonopus canescens;
Tr = Trachypogon plumosus; An = Andropogon
semiberbis.*

This difference may be very significant in terms of
relative changes in population sizes when considering
changes in the environment. If this savanna is burnt 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, Fi+)
and the population should grow. Working with Sporobolus
cubensis, a precocious species from seasonal savannas, we
found that fire not only increases the flowering but also
reduces 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 "r" 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
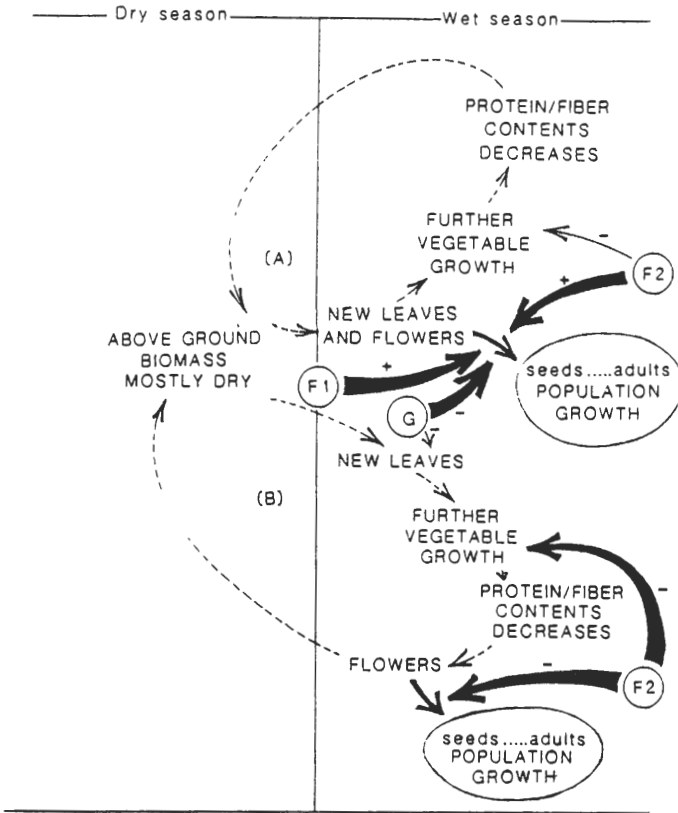not evident.

Fig. 6.2. Simplified diagram of the seasonal growth of
           a precocious (A) and a late (B) species.
           F1, a late dry season fire. F2, a mid to late
           rainy season fire. G, grazing pressure.
           The arrows size suggest the magnitude of the
           effect. See discussion in the text.

If we consider grazing pressures, the precocious
populations will suffer more beause 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-). Late 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-). 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 & Ataroff, 1985) we found several such important relationships between phenology, growth forms and populational 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.

T. 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. semiberbis 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 a 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 lasting. 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. semiberbis represents the first group and T.
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.
semiberbis and A. canescens populations more directly than
T. plumosus populations. The populations may react even
more differently if we consider diaspore 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.
semiberbis (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 (81%). During the
first part of the dry season (January, February), the slope
of survivorship was the same as that during the last part of

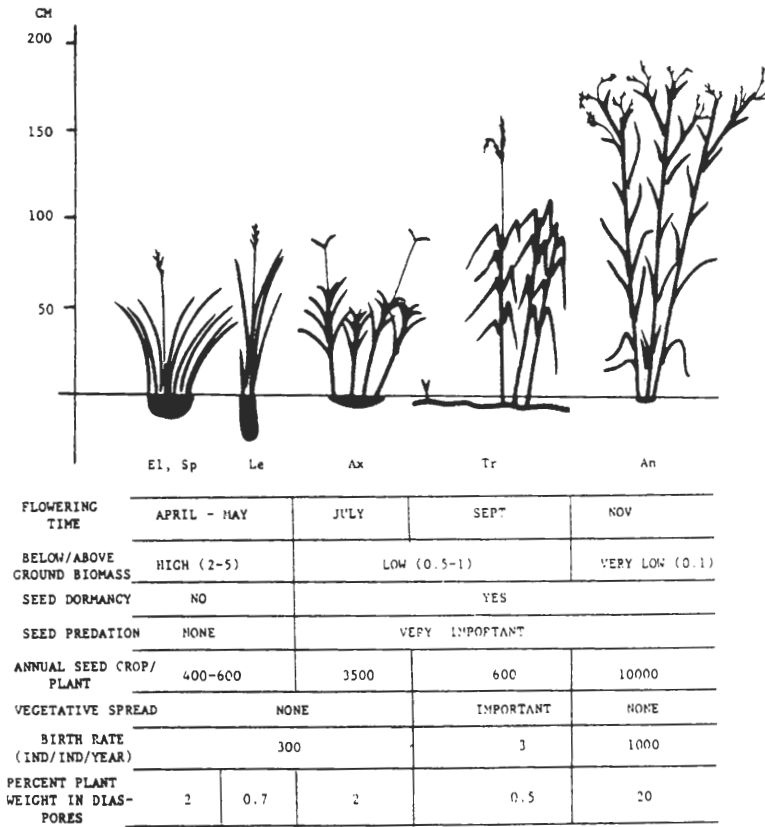| FLOWERING TIME	APRIL - MAY		JULY	SEPT	NOV
BELOW/ABOVE GROUND BIOMASS	HIGH (2-5)		LOW (0.5-1)		VERY LOW (0.1)
SEED DORMANCY	NO		YES		
SEED PREDATION	NONE		VERY IMPORTANT		
ANNUAL SEED CROP/ PLANT	400-600		3500	600	10000
VEGETATIVE SPREAD	NONE			IMPORTANT	NONE
BIRTH RATE (IND/IND/YEAR)	300			3	1000
PERCENT PLANT WEIGHT IN DIAS- PORES	2	0.7	2	0.5	20

Fig. 6.3.   Summary of various traits of six grass
species from Venezuelan savannas. Symbols as
in Figure 1. See text for discussion.
(Silva, unpublished).

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.   semiberbis 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
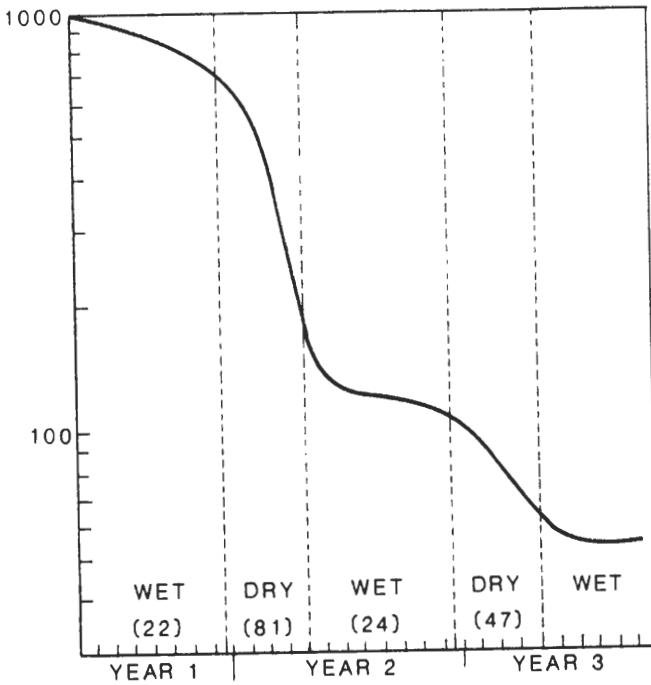has very superficial, short rhizomes and a very low

Fig. 6.4. *Survivorship of a cohort of Andropogon semiberbis. Figures indicate percent of relative mortality between lapses (From Silva, in preparation).*

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 I 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 or 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 demonstrates that the preference of each group is related to water availability for the critical period of flowering and seed set.

Soils	Climate	
	Relatively moist Long rainy season	Relatively dry Short rainy season
Shallow	(May to Nov) Late	(From May-) Intermediate
Deep	(Apr to Oct) Precocious	(May to Oct) Early

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 closer 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 (Walter, 1969; Walker &
Noy-Meir, 1982; Knoop & 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 (Raventos & Silva, 1986). Two precocious bunch grasses Elyonurus adustus and Leptocoryphium lanatum, and a late species Andropogon semiberbis 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. semiberbis 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 asymetric. There are strong competitive interactions between species, but the original hypothesis does not follow. A. semiberbis strongly affects the growth of the two precocious species, and although the effect of
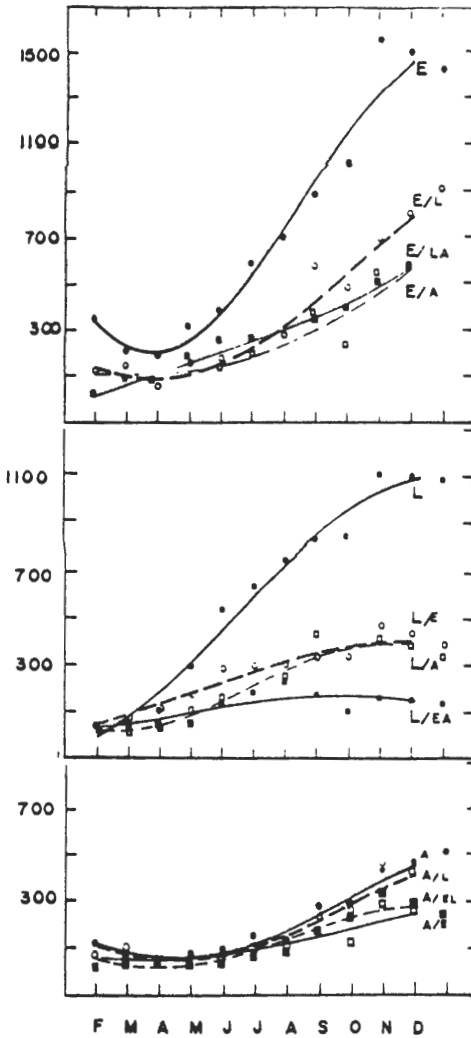
Fig. 6.5.   Changes in plant cover measured throughout
the year in three species, growing alone or
in two and three species mixtures.
E = Elyonurus adjustus;   L =
Leptocoryphium lanatum;   A = Andropogon
semiberbis.   Coverture is expressed in
absolute value and refers to grid
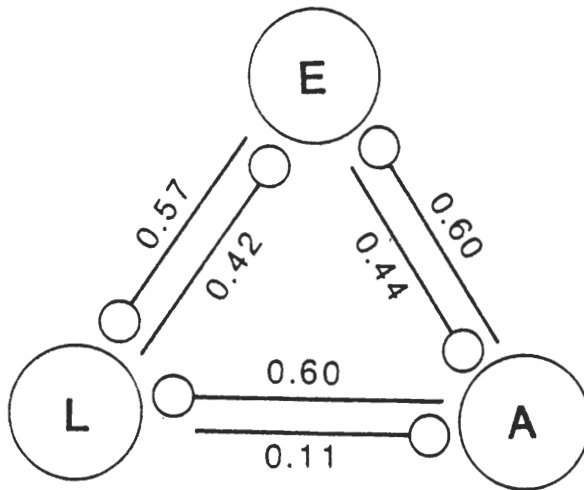interception by foliage.   (From Raventos
& Silva, 1986).

*Fig. 6.6.   Values of competitive interference calculated
from a field experiment in three grass species.
See Figure 5.   (From Raventos & Silva, 1986).*

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 viceversa.
       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, 1981;   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. lanatum have little impact upon the growth of adult
plants of A. semiberbis, 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 till
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 generalized as a
management tool, could be much improved in attempts to
change community composition in desired ways.

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