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RESPONSES OF SAVANNAS TO
STRESS AND DISTURBANCE

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RESEARCH PROCEDURE AND EXPERIMENTAL DESIGN FOR SAVANNA ECOLOGY AND MANAGEMENT

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EXPERIMENT 6, HYPOTHESES 6, 7 AND 8

SPECIES LIFE HISTORIES AND POPULATION DYNAMICS OF SELECTED SPECIES IN SAVANNA COMMUNITIES

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INTRODUCTION

The hypotheses to be tested in this experiment are as follows:

H6. The effect of disturbance on the rate and extent of change in the species composition of a savanna depends principally on the life-history characteristics and population biology of the species.

H7. The responses of savanna species to stress can be predicted on the basis of their life-history characteristics and population biology.

H8. A decrease in the effective rainfall of a site leads to a decline in the species diversity as a result of the loss of species with diverse life-history characteristics.

These hypotheses are concerned with the composition of the savanna community in terms of the functional responses of species based upon their morphological, phenological and demographic attributes, here referred to simply as 'vital attributes' or 'traits' following Noble and Slatyer (1980).

H6 can be tested by identifying sites which differ only in respect of species composition and functional structure, and subjecting them to a standardised type and regime of experimental disturbance. The measurement of the rate and extent of compositional response, can be compared between sites and if these do not differ, the experimental hypothesis will be refuted.

H7 can be tested by formulating predictions on the responses of given populations and communities to a predefined stress. Observations of the responses of the different communities to an experimentally imposed stress can be compared with the predictions.

H8 might be tested as part of experiment 1.

Some problems concerning these experiments need to be discussed. Firstly, we know very little about functional groups of savanna plants and this makes the comparisons and predictions difficult. Secondly, the hypotheses only make sense within a certain range of disturbance and stress intensities. Beyond this range the initial composition is irrelevant since the community undergoes total change. And thirdly, H6 implies that other independent variables are influencing the community response to disturbance to a lesser extent.

To face these problems we consider:

(1) The need to have a simple scheme to classify savanna plants on the basis of morphological and population attributes which allow us to predict their functional responses. Initially this scheme should be as specific as necessary for a particular type of savanna.

(2) The need for experimental changes in the prevalent regime of stress and disturbance to be moderate.

(3) The need to ignore the implications of 'principal effect' proposed in H6. Measurement of the relative importance of other factors such as edaphic and climatic characteristics should be considered in another experiment.

The form that this experiment takes is therefore to propose how the hypotheses might be tested, and to suggest how predictive models might be formulated and tested. The underlying assumptions, experimental hypotheses and null hypotheses are represented symbolically in Table 3.6.1, and the details are discussed below.

Assumptions and predictions

Assumptions and predictions are related to the type of disturbance and stress to be imposed and to the specific community being used. We present here a particular example based on previous work on seasonal savanna communities from Venezuela primarily concerned with the grass component of the herbaceous layer (Silva and Ataroff, 1985; Canales and Silva, 1987; Silva and Castro, submitted).

1. Fire

We now briefly consider the possible ways in which fire might affect savanna plant populations on the basis of two variables: life history patterns and seasonal timing of fire occurrence.

Firstly, let us consider the effects on seeds. Assuming that seeds being produced at the beginning of the rainy season germinate soon after dispersal (such as the seeds of the precocious *Sporobolus cubensis*). Fire should not directly affect them except during the short phase of 2 to 3 weeks between the initiation of flowering and the dispersal phase at the beginning of rains. We assume that species flowering later would exhibit dormancy until the onset of the following rainy season, as shown for *Axonopus canescens*, *Trachypogon plumosus* and *Andropogon semiberbis* (Silva and Ataroff 1985). Hence we expect fire to kill a fraction of seeds in the soil. This effect should be greater on species which are obligate seeders such as *A. semiberbis* than on those species which rely more on vegetative propagation (*i.e. T. plumosus*). The effects on the populations will also depend on the size of the annual seed crop and on the existence of morphological traits protecting the seeds from the fire.

Secondly, let us consider the effects on seedlings. During the critical first months a fire may affect the seedlings of all species similarly, since there has been little time to develop the first rhizome. Survival will depend more on protection afforded by chance factors of the microsite than on specific traits.

Based on measurements of soil temperatures during savanna fires (Gillon, 1983) we will assume that the deeper the meristems of the seedlings in the soil the less damaging the effect of fire will be. Some early species such as *L. lanatum* bury their rhizomes deep in the soil, and we would expect them not to be affected by the fire. On the other hand, other species like *A. semiberbis* have their rhizomes on or above the soil surface making them very susceptible to fire. In this particular species the effect is amplified by the fact that it depends exclusively on seedling recruitment for population growth. But again, this is also affected by the numbers of plants being annually recruited.

These considerations on growth form and phenological differences between plants are relevant to the direct effect of fire on adult individuals. Here, the assumptions and the evidence are not in agreement. We would assume that adult plants of perennial grass species are unlikely to be damaged by fire to any important extent, except perhaps in those species having most of their rhizomes above ground level. However, there is evidence that the vegetative growth of adult plants is impaired in *S. cubensis* which has the rhizomes 2cm deep. Growth is impaired mainly through a decrease in the rate of shoot production after the fire probably resulting from rhizome damage (Canales and

Silva, 1987). Lacey *et al.*, (1982) have suggested that the negative effects of fire seem to be greatest when a fire occurs while the plants are most active physiologically. Therefore, late dry season and early rainy season fires will affect precocious and early species more than the others. Conversely, mid-rainy season fires would affect intermediate and late season species more than the others. However, the interaction of factors in population dynamics adds further complications. The high mortality of adult individuals may affect species with short life cycles less than longer-lived types, because the former recover rapidly from seeds. But this may not operate if adults and seedlings are affected equally. In this case, populations with long cycles and especially those with high vegetative propagation would be least affected.

There is very little information on the indirect effect of fires upon an individual performance. Burning may increase nutrient availability immediately after fire, and this may be positive for precocious and early species growing actively at this time. On the other hand, the moisture status of the soil may be negatively affected because of higher insolation and evaporation from bare soil. Water stress sensitive species would suffer a greater effect than tolerant species. Furthermore, fire promotes flowering of precocious and early species, consequently increasing seed crops. This would cause populations to grow, provided there is no compensating mortality. If adult mortality increases simultaneously, then population turnover will also be increased.

2. Herbivory

We assume that herbivory has selected for species with high investment in defences (chemical and/or anatomical) at the expense of growth and reproduction. Therefore, we predict that an increase in herbivory will affect more palatable species first and will reduce survivorship of seedlings and young plants more than of adults. Species exhibiting strong vegetative propagation and defence mechanisms should then be favoured.

Temporal patterns of grazing would be important in the differential effects upon species with different phenologies as for the effects of fire. Early growers like *S. cubensis* and *Elyonurus adustus* should be more affected by grazing during the beginning of rains than a later grower species. This effect is detrimental upon both vegetative vigor and reproduction since flowering is well synchronized with the growth peak.

Growth form also plays a role in the differential effects of grazing upon savanna grass species. Precocious and early species show a lower ratio of culm/leaf tissue than intermediate and late species, making them more susceptible to grazing specially after a late dry season fire. This should be true even in the case of strong chemical and anatomical defences since they do not fully operate in very young foliage. It seems clear that even under extensive grazing of regularly burnt savannas we should not find precocious and early species lacking in anti-herbivory mechanisms, and that as grazing and burning increase intermediate and late species showing strong culms and vegetative propagation should become dominant.

3. Nutrients

There is unlikely to be much change in overall soil nutrient status independent of moisture. Low nutrient status should exacerbate the problem of drought. Low nutrients will lower growth rate and thereby increase the mortality of seedlings and the lower size classes.

The general conclusion is that stress in savanna should favour K-strategists (*i.e.* plants with a high investment in survival at the expense of reproduction). Vegetative reproduction should be frequent, since vegetatively produced propagules should have lower mortality than seedlings. The greater the stress the more K-strategists should be favoured. Nevertheless, situations can exist where the advantage of K-strategists is decreased. By comparison with r-strategists, the K-types invest more in growth than in reproduction so that factors that impair the energy budget of the latter, making energy investment in growth inefficient, will lower their ability to hold space and resources and lead to a shift towards r-type dominance. Thus, intensive grazing might impair the competitive ability of the K-types, favouring reproduction over growth. Likewise, if the length of the dry season increases, thereby shortening the effective growing season for grasses, a point will be reached where K-types are no longer favoured. An example is the case of the gradient from the Ivory Coast to the Sahelian Region.

IMPLICATIONS

Savannas are presumed to have evolved under frequent stresses of seasonality of water availability, low levels of nutrient availability, periodic herbivory and possibly the recurrence of dry season fire. Under these variable circumstances there have evolved a variety of species which are favoured at various times by different conditions. Management of a constant or regular type is unlikely to be as successful as an event- or circumstance-orientated approach which recognizes the conditions which favour or disfavour desirable or undesirable plant types. A knowledge of the characteristics of savanna plants is therefore critical. Managers will be able to predict how vegetation responds to grazing or burning impacts, thereby enabling them to design strategies which produce or maintain desirable plant species composition. An improved predictive ability also enables the social and economic implications of alternative management strategies to be assessed.

PROCEDURE

Null hypotheses

A null hypothesis appropriate to H6 is that, following a disturbance, the rates and extents of species compositional change will not differ between 2 (or more) sites which differ initially only with respect to plant species composition (expressions (6.8) and (6.9) in Table 3.6.1). This null hypothesis might be considered rejected if the extent of change between sites in response to treatment differs by more than 0.5 species turnovers, and if this between-site difference arises in 5 years or less.

For H7 we will consider that our predictive ability is deficient if our model (expression (6.10) in Table 3.6.1) fails to predict the post-treatment species composition of the vegetation to within some quantitative or qualitative level of accuracy which the researcher must specify. Some examples of specific hypotheses are as follows:

Consider the kinds of changes which we predict will occur under different fire regimes, where the component of fire regime being altered is time of burning (fire intensity will also vary but we assume that its effects are incorporated in, and are less than, those of season of burn). The hypotheses are:

(1) Group (a) species (short-lived, obligate reseeders which flower during the late wet season) will be most susceptible to late wet season/early dry season fires because their seeds are most exposed at that time. Consequently, their populations will decline under a late wet season/early dry season fire regime.

(2) Group (a) species will also decline under an early wet season fire regime because their seedlings are susceptible to fire. Since the adults are short-lived and rely totally on recruitment from annually produced seeds, any factor causing the seedlings to die before they can mature and set seed will inevitably lead to a reduction in population size.

(3) Fires occurring during the late dry season/early wet season will reduce the density of group (b) species. These species either flower precociously or flower early in the wet

season, so that fire at that time will interfere with flowering. Also, they rely to some extent on seed set or recruitment to persist at a site, and fires at the start of the wet season will adversely affect this.

(4) Group (c) plants will decline under a regime of mid-wet season fires because their growth rates, and hence their reproductive rates, are slowed.

(5) Group (d) plants will generally be the most resistant to fire, irrespective of when it occurs.

Our null hypotheses for H8 are that the post-treatment species compositions of experimental and control plots do not differ by more than 0.5 species turnovers (expression (6.11) in Table 3.6.1), and that the post-treatment species richness of the experimental plots is equal to or greater than the post-treatment species richness of the control (expression (6.12) in Table 3.6.1).

Approach

The suggested approaches to testing these null hypotheses are outlined under the introduction above for H6 and H7.

For hypothesis 6, the test outlined below ignores the 'principal effect', and simply addresses the rates and extents of change in plots that differ initially only with respect to species composition.

Design and treatments

At a minimum, 2 kinds of site are needed which differ only in respect of species composition. For each kind of site there should be at least 4 interspersed replications. Some form of disturbance must then be selected (*e.g.* application of nutrients, increase or decrease in effective rainfall, intense herbivory, or change in the prevailing fire regime). If a decrease in effective rainfall is selected, then all 3 hypotheses can be examined simultaneously. This will involve the use of rain-out shelters which, at the cost of about US$4000 each or US$24000 for the whole experiment, probably means that decreasing the effective rainfall as a treatment will only be feasible for the test of H8, for which there must be a control (replicated 4 times) for every site. The selected disturbance, whatever it is, must then be applied uniformly to all the replicates of the 2 kinds of site.

For testing the null hypothesis of H6, the plant species composition must be assessed before treatment, and repeated at annual intervals for 4 or 5 years thereafter. It is suggested that these measurements be done at a standard time, Possibly at the end of the growing season. Demographic analysis should be performed on at least a few selected species. This involves determining annually the size (or age) structure of the population, and recording mortality and natality (vegetative reproduction and seed production) of samples of marked individuals, starting in the growing season preceding imposition of the treatment. The selected plant species should also be classified according to the kind of morphological, phenological and reproductive traits discussed above. The researcher will have to use his knowledge in this regard, depending on the types of plants occurring in his study areas.

Data analysis and interpretation

To test the null hypothesis for H6, the measurements of species composition need to be reduced to a single value or scalar. This can be done by ordinating separately all the annual assessments of the 4 replicates of a site using, say, DECORANA (detrended correspondence analysis). These annual assessments become the samples in the species by samples ordination. If the main axis of variation does not coincide with the apparent species compositional change over time in response to the disturbance treatment, then the validity of H6 can be questioned. If the first axis (or first 2 axes) does account for considerable variation (species compositional change over time in response to the treatment), then the species compositional changes of the plots can be measured as sample scores along the ordination axis (or axes). The difference between the mean positions in ordination space of the 4 replicates of a site prior to treatment and 4 or 5 years following treatment then becomes the scalar of interest (*i.e.* the difference Sa(1)-Sa(2) or Sb(1)-Sb(2) in expression (6.9) in Table 3.6.1). This mean difference has a corresponding variance since there are 4 replicates. Using a t-test we can see whether the mean differences (or distances moved in ordination space in response to disturbance) differ significantly for the 2 kinds of site. The null hypothesis will be refuted if the distances moved differ between sites a and b by more than 0.5 species turnovers. Our rates of species compositional change might be quantified as the number or fraction of species turnovers changed or moved per unit time (in the symbols of Table 3.6.1, dSa = Sa(t+1)-Sa(t)).

A predictive model derived from H7 can be formulated and tested in the following way. First, the data need to be partitioned into 2 sets, one of which is used to build the model, and the other which is used to test it. The partitioning of the data involves randomly selecting 3 of the replicates for the first data set, and reserving the 4th replicate for testing. This partitioning is done once and then applies over all time periods throughout the study so that a given plot belongs in either one or the other data set. Second, using the data collected during the observational period (prior to and following imposition of the disturbance), we set up a matrix classes of growth or demographic responses as heads of columns, and vital attributes as heads of rows. The elements of the matrix comprise frequencies that comply with the cross classification. In Table 3.6.2 an example of the suggested layout is given. A correspondence analysis is then performed to identify which vital attributes are correlated with changes in growth or demography. The researcher may want to try various data transformations, classifications and lumpings of rows. Third, once the correlations are established a quantitative or qualitative predictive model can be formulated. It will probably be easier to develop the latter than the former type of model. It might be a knowledge-based system using IF...THEN logic, viz

(1) IF disturbance X occurs and species A is present and species A has vital attributes V(aa, ab, ac, ...aj) THEN the species will increase (or decrease or be exterminated or be maintained or whatever).

(2) IF disturbance X occurs and species B is present and species B has vital attributes V(aa, bb, bc, ...bj) THEN then the species will increase (or decrease or be exterminated or be maintained or whatever).

Several iterations of model development, assessment of model fit to the first data set, and model refinement will probably be necessary.

The fourth step is to test the model by applying it to the reserve set of data to see if it predicts the observed changes.

In the case where the effective rainfall has been experimentally decreased (H8), we can resort to t-tests to examine the significance of any differences in species composition and species richness between the experimental and control plots. Again, the data on species composition will have to be reduced from vectors to scalars, and again ordination might be used to produce sample scores on ordination axes.

Table 3.6.1 Symbolic representation of the assumptions, experimental hypotheses and null hypotheses for experiment 6.

Assumptions

For hypothesis 6 we assumed that

$$dS/dt, S(1)-S(2) = f(S(1)) \tag{6.1}$$

where,

S is the plant species composition,
t is time,
S(1) is the initial or pre-treatment plant species composition, and
S(2) is the post-treatment plant species composition.

For hypothesis 7 we assume that

$$S(2) = f(T, S(1), V(1), V(2), V(3), \ldots V(J)) \tag{6.2}$$

where,

T is the nature, timing and severity of stress or disturbance, and
V(1), V(2), V(3) ...V(J) are vectors characterising the vital attributes of species 1, 2, 3 ...J comprising the pre-treatment flora S(1).

For hypothesis 8 we assume that

$$S,R = f(M) \tag{6.3}$$

where,

R is the species richness, and
M is a measure of moisture availability over the growing season.

Experimental hypotheses

From hypothesis 6 we predict that the rates of change on 2 sites a and b are going to differ

$$dSa/dt \neq dSb/dt \tag{6.4}$$

where,

Sa is the species composition of site a, and
Sb is the species composition of site b which is similar to site a in all respects save in initial species composition.

We also predict that the extent of plant compositional change between sites a and b are going to differ:

$$Sa(1)-Sa(2) \neq Sb(1)-Sb(2) \tag{6.5}$$

From hypothesis 7 we predict the post-treatment plant composition on the basis of a model (expression (6.2)) of the vital attributes of the species initially present.

From hypothesis 8 we predict that a decline in effective rainfall will result in the plant composition and the species richness of the experimental site being different to and less than the values for the control:

$$Se(2) \neq Sc(2) \tag{6.6}$$

and

$$Re(2) < Rc(2) \tag{6.7}$$

where,

Se(2) is the post-treatment plant species composition of the experimental plots,
Sc(2) is the post-treatment plant species composition of the control plots,
Re(2) is the post-treatment species richness of the experimental plots, and
Rc(2) is the post-treatment species richness of the control plots.

Null hypotheses

For hypothesis 6 we have the negation of expressions (6.4) and (6.5), namely that the rates of change in composition between sites a and b following a disturbance will not differ:

$$dSa/dt = dSb/dt \qquad (6.8)$$

and that the extent of change between sites a and b also will not differ:

$$Sa(1)-Sa(2) = Sb(1)-Sb(2) \qquad (6.9)$$

Hypothesis 7 will not hold if we are unable to predict the post-treatment composition from the vital attributes of the species initially present

$$S(2) = f\,(T, S(1), V(1), V(2), V(3), \ldots V(J)) \qquad (6.10)$$

For hypothesis 8 we have the negation of expressions (6.6) and (6.7), namely that post- and pre-treatment species compositions will not differ

$$Se(2) = Sc(2) \qquad (6.11)$$

and that the post-treatment species richness will be equal to or greater than the pre-treatment species richness

$$Re(2) \geqslant Rc(2) \qquad (6.12)$$

Table 3.6.2 Proposed matrix for establishing possible correlations between morphological, phenological and reproductive attributes of plant species with their demographic responses to a given type of disturbance.

	TIMES OF SURVEY AND PLOTS		
	PRE-TREATMENT SURVEY	POST-TREATMENT SURVEY 1	POST-TREATMENT SURVEY 2
	PLOT1 PLOT2 ...	PLOT1 PLOT2 ...	PLOT1 PLOT2 ...
DEMOGRAPHIC PARAMETERS			
Mortality:[1]			
class 0			
class 1			
....			
class n			
Vegetative reproduction:[1]			
class 0			
class 1			
....			
class n			
Sexual reproduction:[1]			
class 0			
class 1			
....			
class n			
Population size:[2]			
class 0			
class 1			
....			
class n			
MORPHOLOGICAL CLASSES	(Categorize plants into appropriate classes)		
PHENOLOGICAL CLASSES	(Categorize plants into appropriate classes)		

[1] Record a value for each time period for each plot for each selected species for each class.

[2] Record density or an index of it for each time period for each plot for each selected species and for each class.