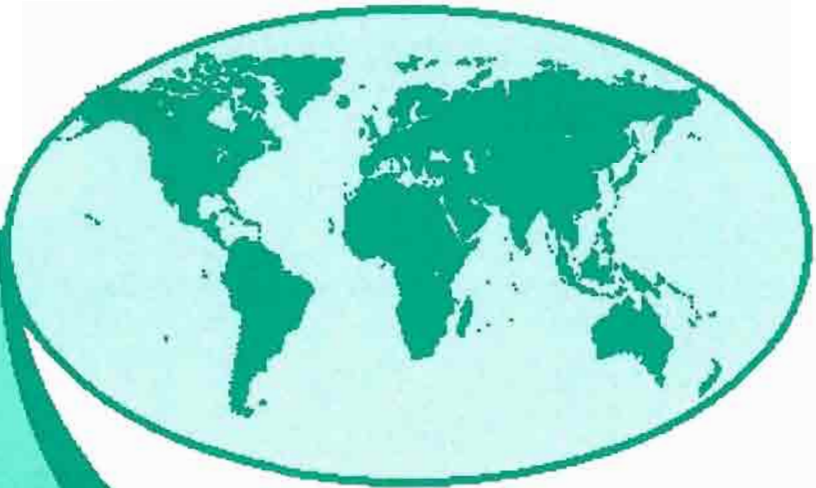
IUBS

UNESCO

SAVANNA MODELLING FOR GLOBAL CHANGE

Edited by Otto T. Solbrig



Biology International

Special Issue N° 24

SAVANNA MODELLING FOR GLOBAL CHANGE

Report of a Workshop held at the Harvard Forest,
Petersham, Mass. U.S.A., 15-20 October, 1990

Edited by Otto T. Solbrig

with the collaboration of

Jean-Claude Menaut
Mike Mentis
Herman H. Shugart
Phillip Stott
David Wigston

Special Issue N° 24
BIOLOGY INTERNATIONAL
The International Union of Biological Sciences
News Magazine

TABLE OF CONTENTS

1. Introduction

2. Questions

3. Importance of PAM & PAN: a Function of Spatial/Temporal Scales 6

4. Hierarchy Theory and Grass-Tree Interaction 18

5. Approaches to Modelling Savannas 29

6. RSSD and Global Change: Higher Order Interactions 36

References 42

List of Participants 46

SAVANNA MODELLING FOR GLOBAL CHANGE

1. INTRODUCTION

1.1. Importance of tropical savannas. Two thirds of the world's population inhabit the tropics, mostly savannas or former savanna lands. Many of these people live in rural societies that depend on subsistence agriculture. Currently profound changes in the composition and productivity of tropical savannas are taking place around the globe. These alterations may adversely affect the capacity of these systems to support humans and their domestic animals. These changes are part of the more general and wider problem of global environmental change including ozone depletion, global warming, waste disposal, deforestation, and species extinction.

In 1983 the International Union of Biological Sciences (IUBS) concerned about the rapid transformation of tropical landscapes, initiated jointly with the Man and the Biosphere Program of UNESCO a ten-year investigation into tropical problems (Solbrig and Golley 1983). As part of this effort it develop the program called "Responses of Savannas to Stress and Disturbance" (Frost et al. 1983). The goal of this project is to develop an understanding of the way tropical savannas respond both to natural and to human stresses and disturbances. Such knowledge is pursued through a comparative analysis of selected aspects of tropical savannas.

1.2. Definition of and Physiognomy of tropical savannas. Savannas are tropical systems intermediate between dry, xerophytic woodlands and moist deciduous forests. They comprise a distinct biome characterized by the presence of a continuous canopy of graminoids, principally C4 grasses and sedges, and a discontinuous canopy of trees and shrubs. The woody elements may be rare or even absent under certain circumstances, or they may be represented entirely or primarily by shrubs.

Savannas are found in all tropical areas of the world, occupying perhaps 40% of the tropical land surface. Their great physiognomic variability coupled with their distinctive characteristic namely the coexistence of trees and grasses, have intrigued ecologists for a long time. The diversity of savannas have induced copious explanatory hypothesis and a good share of controversies (Beard 1953; Hills 1965; Bourliere and Hadley 1970). Thus from both a scientific and land management viewpoint, there are a variety of reasons why tropical savannas are an important research subject. Some of these are:

The increasingly intense use of savannas by an expanding human population which is resulting in significant changes to the soil and vegetation. When combined with natural stresses such as drought, these changes are leading to increased erosion and aridification of the soil. Research into the causes and consequences of these changes in savannas could help alleviate some of these problems in the future.

Within the tropics, the coexistence and close interaction of the woody and herbaceous strata makes savannas unique. Both strata are of economic value and a better understanding of the reasons for this coexistence should contribute to improved land management (Walker 1987; Sarmiento 1990).

Savannas are one of the most seasonal of the world's major biomes, experiencing strongly contrasting climatic conditions within a year, as well as high variability between years. They also display a great deal of spatial heterogeneity. This creates a constantly varying environment for the biota and is probably a major factor in enabling a relatively large number of species of contrasting life forms to coexist. They are therefore ideal systems in which to study how plants and animals cope with the stresses of a variable environment. They are also good places to acquire a better understanding of the effects of human induced stresses in these and other ecosystems.

Fire, frequently associated with human activities is a prominent feature of most tropical savannas (Stott 1988). It affects the functioning of these systems in a variety of ways. Since fire can be managed, a better understanding of its ecological effects, would be extremely valuable.

In view of the uniqueness of the set of ecological interactions that determine the existence of these systems, further advances in ecological theory can be expected from their investigation. Over the past few years there have been several detailed syntheses of the results of research on savannas in different parts of the world (Hills and Randall 1968; Bourliere and Hadley 1970; UNESCO 1979; Walker 1979; Huntley and Walker 1982; Bourliere 1983; Sarmiento 1984; Stott 1984; Tothill and Mott 1985; Frost et al. 1986; Sarmiento 1990). These syntheses provide a foundation on which to build a comprehensive theory of savanna structure and function.

1.3. The objective of the meeting. Progress within the RSSD program calls for more precise explanation of the coexistence of grasses and woody plants and their dynamics through time. It also calls for estimates of the changes in savanna structure, composition and functioning likely to occur in response to stresses and disturbance. The extensive changes taking place worldwide as a result of increased human activity (Solbrig 1990) are likely to have a severe impact on savannas. There is increasing alarm that the planet Earth will experience global climatic change in the next 50-100 years in response to the increase in atmospheric greenhouse gases caused by human activity. The effect of these changes on the biota and vice-versa is now being studied by an international research program known as IGBP (International Geosphere-Biosphere Program).

As part of the development of the RSSD program a small workshop of experts was convened at the Harvard Forest in Petersham, Mass., U.S.A., from October 15-20, 1990. The objective of the workshop was to examine in greater detail the relation of moisture and nutrients to savanna structure, especially the tree/grass association, and to investigate the possibility of modelling the growth of tropical savannas. Another objective was to explore how savannas might be impacted by predicted climatic changes, and how changes in savannas in turn may impact global climatic change. Another objective was to explore whether fruitful research linkages with IGBP can be established.

The assembly (see appendix 1) listened to some general presentations and then divided into two groups that discussed four principal questions: (1) the role of savanna determinants, especially Plant Available Moisture (PAM) and Plant Available Nutrients (PAN); (2) ways to measure PAM and PAN; (3) the hierarchical nature of savanna determinants; and (4) approaches to savanna modelling. The result of eachgroup's deliberations were communicated to the entire assembly, and then reported in writing. The present communication is an edited version of the proceedings of the workshop.

1.4. Introduction to modelling. Models fall into two categories: predictive and explanatory. Predictive models are designed to prognosticate the future state of complex systems. Although these models often incorporate mechanistic descriptions of system processes, it is the quality of prediction that matters. Thus, they tend to incorporate empirical and locally specific information.

Explanatory models are designed to assist scientists explore complex hypotheses. Ideally these explanatory models mimic closely the essential structure of the system being modelled by using mechanistic descriptions of system functioning and a minimum of empirical information. The user is concerned with the interrelationships between the components of the model and its comparative performance over a broad range of conditions.

Although a modeler may attempt to develop a model for both explanatory and predictive purposes, the outcome will be a compromise in which some aspects of one purpose are traded-off against aspects of the other. An essential first step in designing a new model, or assessing an existing one, is to decide on the main purpose of the model and to act accordingly.

Progress within the RSSD program requires both explanation and prediction: explanation of such features as the coexistence of grasses and woody plants, and their dynamics through time; prediction of the likely changes in savanna structure, composition and functioning in response to stresses and disturbance.

2. QUESTIONS

2.1. Principal questions. The RSSD study of savannas, particularly any modelling efforts, are motivated by three key questions:

What factors control processes in savannas across regions and among continents, at a range of spatial and temporal scales?

This question relates to the hypotheses underpinning the RSSD program (Frost et al. 1986; Walker and Menaut 1987). Modelling can be used to simulate the dynamics of tree/grass interactions; changes in plant spatial distributions, as influenced by seed dispersal and establishment, soil moisture, herbivory, and fire; plant production processes; the interactions of herbivory and fire; and many other physiological, population, and ecosystem processes.

How will savannas change at different spatial scales in response to anthropogenic and natural stresses and disturbance?

This question is central to the issue of the effects of global climate change on savannas. To be effective, the models of savanna functioning must not only be able to simulate the effects of changes in land-use and physical disturbance, but also the effects of changes in rainfall regime (particularly the annual amounts, seasonality, the frequency of rare events - extreme droughts or wet years - and the frequency distribution of features such as storm intensities), carbon dioxide levels, and temperatures.

Variables which would be expected to respond to such changes include grass and woody plant biomass; the grass/woody ratio; vegetation structure; species composition or plant functional types, or both; regional hydrology and the redistribution of water and soil; and carbon and nutrient pools and fluxes.

How will changes in savanna structure and functioning affect inputs to global climate models?

Key issues posed by this question include savannas as a source or sink of carbon; patterns of trace gas production and absorption; changes in evapotranspiration; changes in shortwave reflectivity (albedo); and changes in surface roughness. The outputs from any models which address this question must be generalizable over large spatial scales in order to link effectively with global climate models. Such models are currently parameterized on a 200 x 200 km grid.

3. IMPORTANCE OF PAM AND PAN: A FUNCTION OF SPATIAL/TEMPORAL SCALES

3.1. Initial Considerations. It has been hypothesized (Walker and Noy-Meir 1982; Frost et al. 1986) that the balance between a continuous grass cover and a discontinuous stratum of woody plants (trees and shrubs) is above all determined by the availability to the plant of soil moisture (PAM) and nutrients (PAN). Savannas occur in environments with manifest moisture discontinuities throughout the year and low soil nutrient content (Bourliere 1983). There are however great differences between regions in rainfall, length of the dry season, and soil nutrient content. Savanna ecosystems also show a diversity of structural and functional characteristics. This complicates classification of savanna types. Classifications based solely on physiognomy are unsatisfactory because they do not reflect the numerous functional types.

We consider (Frost et al. 1986; Goldstein and Sarmiento 1987; Medina 1987; Walker and Menaut 1988) that variation in soil moisture and soil nutrient availability are major reasons for the diversity of savanna types. We therefore feel that if a satisfactory index of soil available moisture (PAM) and of soil available nutrients (PAN) can be developed, it would be possible to produce a classification of the world's savannas that reflects their functional differences. Yet such measures are not easily obtained.

3.2. Definition and Meaning of the PAM-PAN Plane. Savannas are heterogeneous systems, covering a wide range of soils and climates and exhibiting a range of vegetation structures and functions. Because of this it is difficult to extrapolate understanding developed at one site to another. Additionally, in terms of the requirements of the IGBP, we need to characterize savanna types in terms of the seasonal course of evapotranspiration, albedo, gas exchange and surface roughness, and how particular savannas will respond to global change. These dynamic predictions require detailed mechanistic models which will be too complex to run for every location in the savannas. There is thus a need for a satisfactory common basis on which to identify distinct savanna types, their global distribution, and what initial parameter values complex models will assume. For these reasons we require a framework for classifying the savannas of the world on the basis of their primary determinants.

Until this workshop, RSSD participants had worked on the basic hypothesis that soil moisture and nutrient availability are the primary determinants of savanna functioning, and that their variation in space and time are the principal reasons for the diversity of savanna types (Frost et al. 1986). Consequently it was hypothesized that the world's savannas could be differentiated by their location in the plane defined by plant available water and plant available nutrients. The problem was to define indices of moisture and nutrients (Walker and Menaut 1987), since simple indices such as rainfall and soil type had proven insufficient. As a result of discussions at this workshop, it is now considered likely that temperature (T) will need to be included as an additional variable, especially when working at a small scale. This needs to be researched further by detailed examination of the most effective ways of characterizing PAM, PAN, and T and how they determine vegetation structure. If this can be successfully achieved then a number of inferences can be drawn about savanna functioning and the manner of response to changes in climate, land use, and disturbance regime. Once the validity of these relationships is established, a second objective is to develop procedures that will enable us to place any savanna within the PAM-PAN-T space using information which is readily available at a global scale.

3.3. PAM and PAN in a spatial/temporal context. One of the fundamental problems is scale. At any given spatial scale the rates of key processes and the response times of the vegetation to different inputs will determine the types of measurements taken, the methodology employed and the necessary interval between successive measurements.

Spatial/temporal scales are nested. For example, seasonality occurs against a backdrop of interannual variability; interannual variability occurs against a backdrop of less frequent more catastrophic events such as drought, frost, pathogen/herbivore irruptions, etc. These latter forces may determine the structure and function of a savanna system for long periods thereafter. Although these episodic events are infrequent, they occur with a fair amount of certainty and inevitability.

Processes operating at a high frequency at a local scale are embedded within forces which operate at lower frequencies over larger spatial scales. Thus, as one goes upward in a spatial/temporal hierarchy, the higher levels contain and constrain the lower levels.

The driving force for change in savannas may result from a shift in the mean values of key driving variables in PAM, and PAN, and/or a shift in the variation about these means, and/or a shift in the magnitude and/or frequency of the extremes. Furthermore, infrequent, broad-scale forces that drive key processes in some regions may not operate in others (e.g., El Niño\La Niña events). Long term observations are needed to ascertain whether savanna systems are undergoing fluctuation, cyclic replacement or directional change.

Figure 1 is a graphical representation of the relation of PAM and PAN to phenomena occurring at different temporal and spatial scales. The horizontal axis represents a gradient of relative spatial scales within which are defined patches, catenas, landscapes and biomes. These categorical designations of space are relative and their absolute size varies from location to location. The other axis, time, is also relative rather than absolute. It represents responsiveness of the system components at various scales to various forces, either periodic or aperiodic. The rate at which key processes occur will dictate appropriate sampling procedures and sampling intervals. Response times at the patch scale might vary from short-term through to long-term, but short-term responses would be expected to occur with a high frequency. As the geographic scale increases (cartographically from large to small) response times are likely to become progressively longer.

The diagonal line in the graphical representation relates temporal response to relative scale, and superimposes on this the primary vegetation characteristics of each relative scale. At the patch level, we are concerned primarily with species composition, whereas at the catena scale functional groups assume greater importance. At the landscape scale, physiognomy emerges as a distinguishing trait, and formations at the regional scale.

3.4. Definition of Geographical Scale Divisions.

Patch - Usually a small area which is homogeneous in relation to some chosen characteristic such as vegetation (grassy patch, tree patch, shrub patch), topography (flat patch, slope patch, plateau patch), or soil characteristic (sandy patch, clay patch), or animal activity (ant hills, termite mounds, animal territory). Savannas below the landscape level may consist of a mosaic of patches in which PAM and/or PAN may vary. Each patch may vary in size from as small as an ant hill or individual tree crown up to the size of a landscape unit. Processes forming patches may result from the dynamics of the vegetation and/or fauna, or they may be determined by external events such as anthropogenic disturbance, catastrophic fires, storms, etc. The relative importance of patch-forming processes may depend on savanna type.

The temporal response scale of most patch-forming processes is frequent and of short-term duration, although some infrequent, long-duration patch-forming events may also occur. In savannas subject to infrequent human disturbance, most patch-forming processes are the result of the internal dynamics of the system.

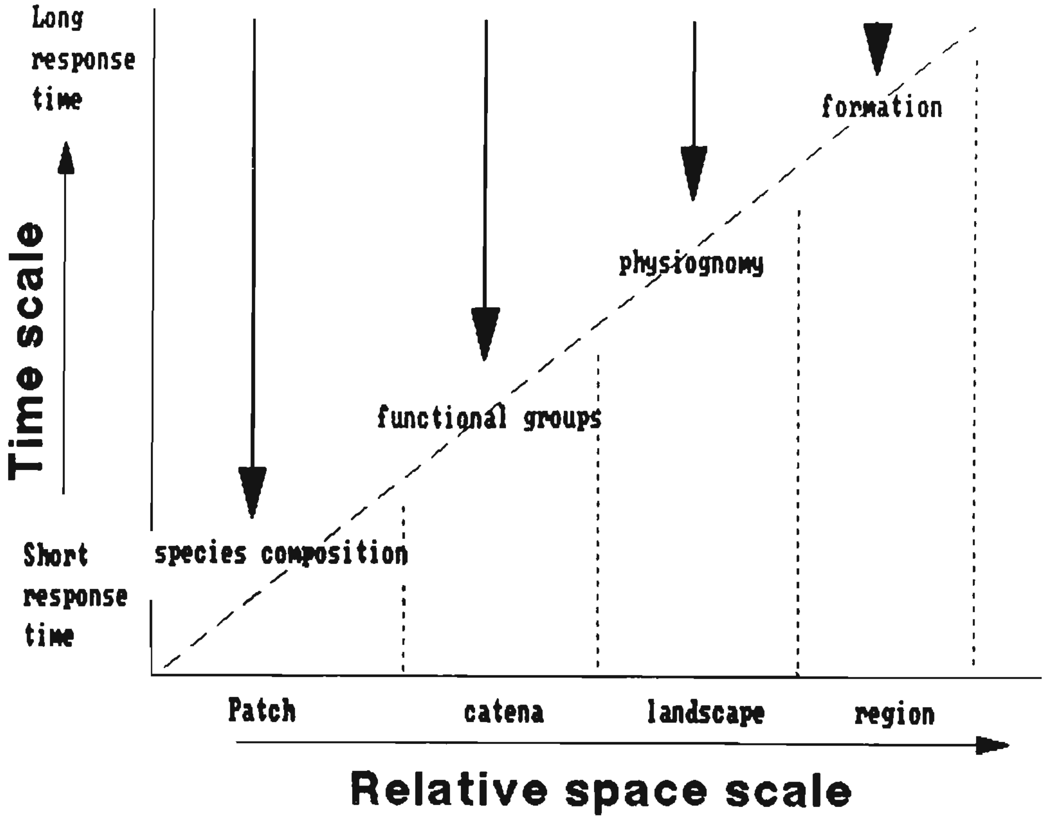


Figure 1. A diagrammatic conceptual framework for evaluating PAM and PAN at various spatial and temporal scales. The horizontal axis represents relative spatial scales; the relative range of temporal responses at each spatial scale is represented by the vertical axis. Structural levels are depicted in the diagonal.

Catena - a topographically determined landscape unit in which a series of patches may be linked through a continuum of processes. In practical terms, this often means a linear transect along a clearly determined environmental gradient. Three categories of patches might be recognized within the catena level of organization: run-on patches, run-off patches and their transition zones. In dry savannas run-off patches may be dominated by herbaceous vegetation and small shrubs, whereas sufficient water may accumulate in run-on patches to support larger shrubs or trees. Transition zones may be characterized by some intermediate combination of lifeforms or growthforms. For modelling purposes and hierarchical continuity, catenas are homogeneous with respect to factors like rainfall, soil system, etc. which will vary at higher levels of organization. However, within the catena, variation in soil properties (notably texture and nutrients) will mediate PAM, PAN and patch structure.

Landscape - a topographical area, geomorphologically determined, geographical unit; a contiguous set of catenas. Some landscapes are easily mappable, having clearly defined boundaries (such as watersheds). In other cases their delineation is rather arbitrary. Landscapes with distinctive features have often derived those features from a subtle interplay of physical and biological factors. In landscapes, the lateral movement of H_2O is often an important PAM-related process. At the landscape level of organization, factors associated with basin hydrology (soil moisture storage, ground water/aquifer variation, stream discharge, sedimentation, etc.) often arise as important controlling factors.

Region - Regions are comprised of sets of landscapes which are sorted by rainfall regimes and geomorphology. They may constitute land-use areas, territories, geopolitical designations (parks, reserves) etc.

3.5. Faunal component. As presented, figure 1 applies only to vegetation. The faunal component should also be integrated appropriately at various spatial and temporal scales. Vegetation provides habitat and resources for animals thus influencing their distribution and abundance. Animals, in turn, may be a potentially important determinant of PAN via their effects on nutrient redistribution and availability. Animal activities contribute to patch formation and also influence the rates and dynamics of processes within patches, between patches along a catena gradient, and across catenas and landscapes. Animals may accentuate or intensify heterogeneity up to a certain point, beyond which excessive activities may induce homogenization (e.g., intermediate disturbance-type concept). As populations increase the human role in mediating the impacts of other animals becomes increasingly important (Sinclair & Norton Griffiths 1980; Menaut et al. 1985; McNaughton 1985; Abbadie & Lepage 1989). The elimination or enhancement of native browsers, grazers and granivores (directly or indirectly) and/or the introduction of livestock in sufficient numbers and concentrations can interact with abiotic forces to substantially alter the grass/shrub/tree balance through time (directly as via primary production or indirectly as by causing change in fire regime, Archer 1990). Shifts in forest-savanna boundaries and changes in the areal extent of gallery forests have the potential to affect faunal diversity (Fig. 2).

Scales of faunal spatial activity are theoretically proportional to body size, metabolic rate, trophic level, group size and primary productivity, whereas scales of faunal temporal activity are proportional to generation time and related demographic variables (Fig. 3). Different animal groups occur in different portions of the spatio-temporal plane, with endothermic vertebrates generally operating on a coarser scale than invertebrates, but with ectothermic vertebrates tending to operate on a longer time scale due to their lower metabolic rates.

3.6. Measuring PAM and PAN at different scales: external drivers versus endogenous controls. Earlier we argued that PAM and PAN were the primary determinants of savanna structure. The question then is "how do these forces interact at various spatial scales ranging from the patch upward to the catena, the landscape, and the region?"

We contend that external forces act upon savanna components across an array of spatial and temporal scales to influence the rate and magnitude of ecosystem processes and responses. Given that a hierarchy of dynamics exists, at what scale(s) is the PAM-PAN plane most germane? At what scale does PAM-PAN reflect external drivers and endogenous controls over savanna processes or responses? At large spatial scales and long time frames, climatic factors and geomorphology may dictate savanna structure. However, as spatial resolution is increased and time frames diminished, biotic processes and local topo-edaphic features may become increasingly important.

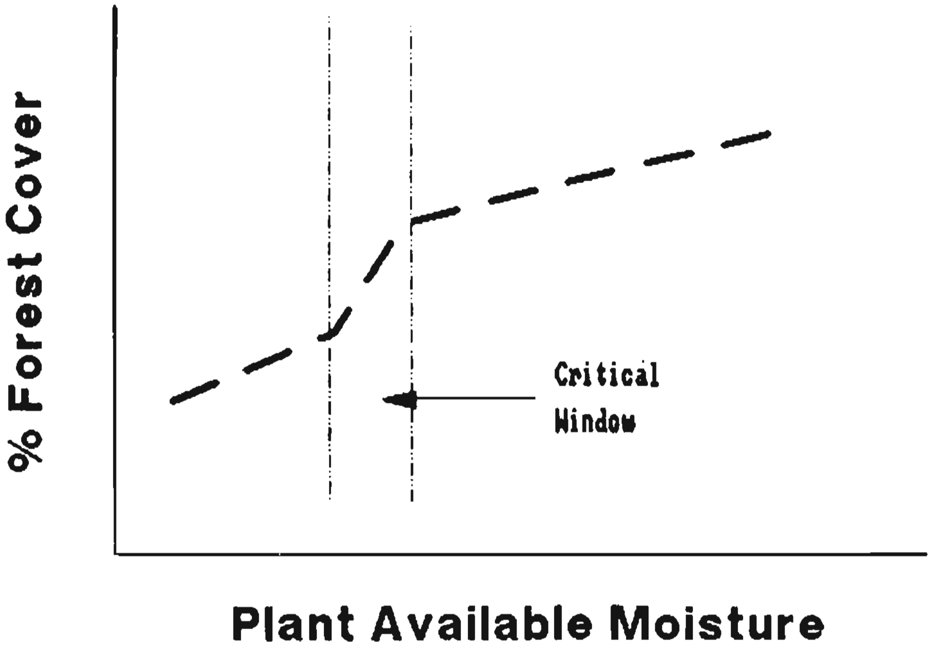


Figure 2. Graphical representation of possible influence of moisture regime on the forest-savanna boundary and consequently on animal diversity at landscape scales. The critical window represents the forest-savanna boundary.

The patterns of "patches" in savanna systems (their dimensions, their state at a given time and their arrangement and boundaries) are a complex consequence of (1) a web of processes interacting with one another within the patch locale, and (2) the antecedent conditions that make up the history of each patch. One important consideration in understanding how the PAM-PAN concept interacts with savanna patch dynamics is the relative contribution of those two factors. Tansley (1935) wisely retracted his distinction between allogenic and autogenic forces in succession in the paper in which he coined the term "ecosystem." We are not attempting to revitalize that argument here. Rather, we suggest by

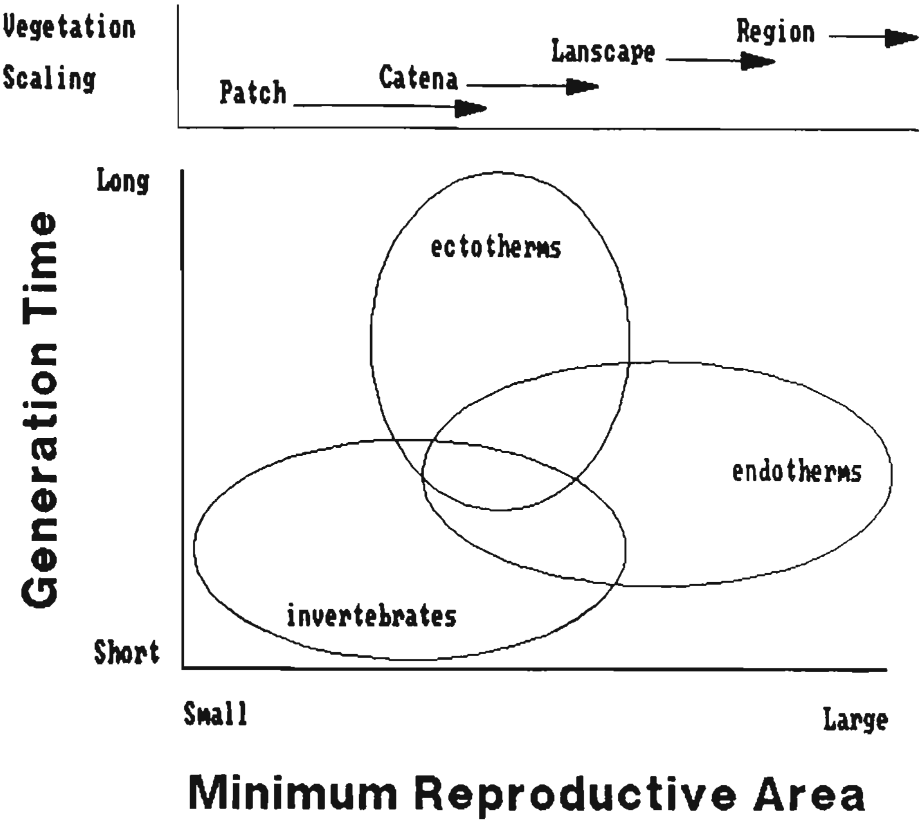


Figure 3. An attempt to relate animal activity to spatial and temporal scale considered in savanna studies. Minimum Reproductive Area (MRA) for animal species is an index of spatial activity which utilizes body size, metabolic rate, diet, reproductive group size and primary productivity. MRA is the area sufficient for a species to successfully reproduce and persist through more than one generation (Braithwaite 1984) . Scale of temporal activity is proportional to generation time which is related to other demographic variables.

analogy the traditional method of solving differential equations by separating the solution into parts with and without explicit functions of time. A particular solution is, of course, only specified when both parts are known. The considerations are: (1) Would a savanna mosaic form on a homogeneous substrate from system feedbacks? (2) To what extent are patches stable, unstable or chaotic? (3) For unstable patches, are intrinsic dynamics moving a given patch type toward a single equilibrium end point or toward one of several possible equilibrium states? (4) Do disturbances, climatic variation or other factors synchronize or initiate the dynamics of patches? (5) What factor(s) control patch size, shape and boundary characteristics? The answers to these questions will vary to some extent, depending on the spatial and temporal scale under consideration. One manner of resolving this confusing and confounding situation is to consider the space and time domains of three sorts of important factors:

Externals - factors whose behavior can be treated as being a function of time.

Processes - interactions among objects that comprise the system of definition.

Responses - behavior of the system of definition as a consequence of interactions between externals and processes.

This time/space domain is represented conceptually in Fig. 4. It is important to note in this context that a particular phenomenon can occupy any of the three domains at different temporal and spatial scales. For example, a wildfire might constitute an external with respect to a small patch of land, as a response in the fire pattern caused by fuel distributions at the landscape scale, or as a process that can always be expected to be omnipresent on a large landscape over a longer time frame. The levels in Fig. 1 are thus interpreted within this context.

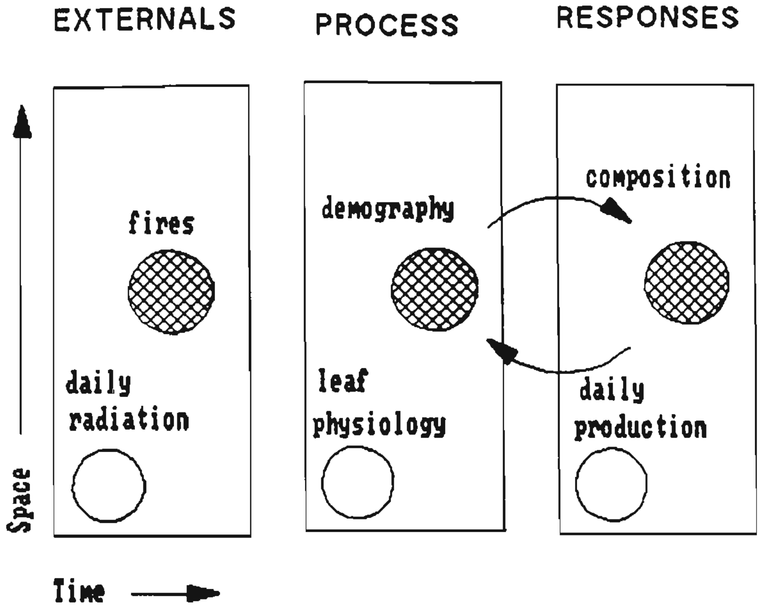


Figure 4. Representation of the three factors (externals, processes and responses) and their relations in space/time domain. Two phenomena are represented. In the first, daily radiation interacts with leaf physiology to produce daily production in a centimeters to meters x seconds to hours space/time domain. In the second fires interact with plant demography (phenology) to result in species composition in a year to decade x landscape to region time/space domain.

3.7. To what extent are PAM and PAN independent single measurements? PAN may be subservient to PAM and regulated by the seasonality and amount of moisture. Levels and the dynamics of PAN may be largely driven by patterns of moisture input and wet/dry cycles. PAM-

PAN interactions would be mediated by factors such as temperature (which influences microbial activity) and pH (as it influences mobility).

To what extent can PAN be represented as a single measurement or as some form of an integrative index among tropical savannas? The relative pool size and turnover rate of plant-available N, P or various micronutrients may vary between savannas and it is difficult to make generalizations. Specifically:

Different nutrients have different rates of cycling and thus respond at different time scales. Differences in solubility and mineralization would influence the rate and magnitude of translocation, laterally and vertically.

Multiple limitations. In a given system, supplementation of either water or N or P may elicit a response.

The individual plants in a particular location may be limited by different factors to different degrees. For example, a tree might require water to balance its heat budget by transpiration whereas the grasses beneath the tree might require light or nitrogen.

Different nutrients have different functions in the metabolism of plants and animals and thus the effects of their shortages or abundances can vary with elements and chemical species.

3.8. Necessary Information. The smallest spatial scale considered is the patch, a relatively small area (but of no absolute size) which differs in species composition, biomass or some other crucial characteristic from the surrounding matrix of vegetation. Within the patch, soil water potential is presumed to be the key variable which integrates a variety of factors governing patch dynamics. Although patches may arise from a variety of causes, a particularly important element of savanna structure is the dichotomy between run-off and run-on "facets" or patches (Fig. 5). In this formulation, run-off areas support distinctly different vegetation types than patches receiving run-on. For purposes of modelling, these portions of landscapes are thus treated as distinct units. In dry savannas, run-off patches support herbaceous vegetation, whereas run-on areas support shrubs or trees. In other cases, run-on areas may support tall grasses or species tolerant of salinity or periodic flooding whereas run-off areas would contain short grasses. The distinction between run-on and run-off areas may diminish in wet savannas, or on landscapes where there is little topographic relief.

With respect to the measurement of vegetation responses, the following variables are considered necessary:

(a) Tree cover (at all scales).
(b) Stature of key plant forms (trees, shrubs, grasses) and vertical/horizontal stratification.
(c) Balance among lifeforms in terms of leaf area and below ground biomass. This information may not always be available.
(d) Boundaries (patch interfaces; savanna-forest interface).

(e) Fire frequency (a potential function of PAM at scales above catena); also a key variable that has bearing on global atmospheric chemistry).
(f) Areal extent of gallery forest (above catena level).

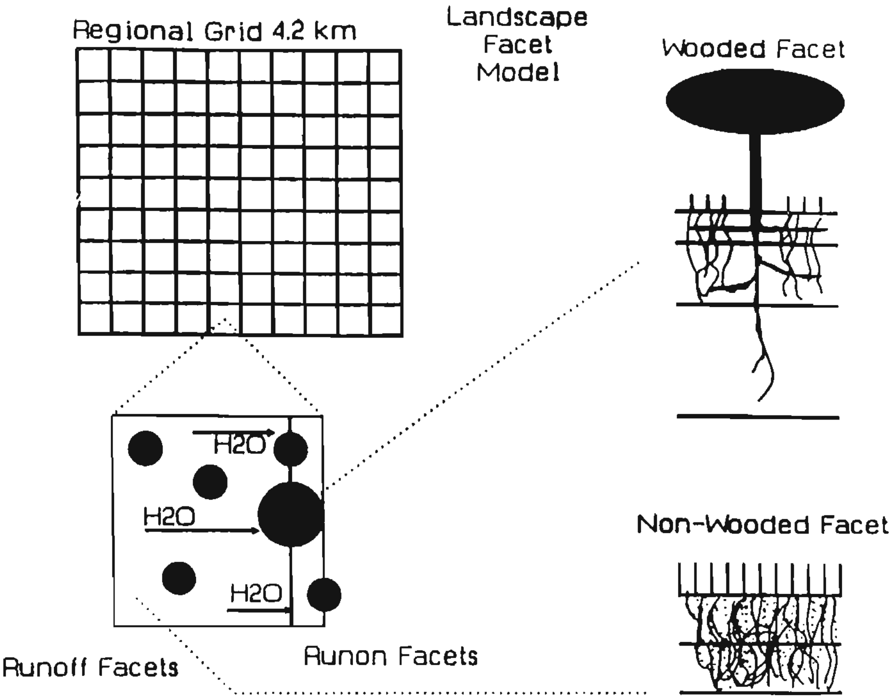


Figure 5. Nested spatial structure for modelling effects of micro topography and run-off on savanna vegetation at catenary, landscape and regional scales (from M.B. Coughenour, unpublished)

3.9. Inferences which may be made from PAM-PAN Plane. If the PAM-PAN model successfully captures a major portion of the variation of structure in savannas, then there is good reason to expect that the following structural and functional characteristics, all of great consequence to the IGBP program, will also be predictable. The testing of this hypothesis constitutes a second phase of the PAM-PAN project:

(a) total carbon stocks in the soil and plant components;
(b) seasonal time course of evapotranspiration;
(c) seasonal course of albedo;
(d) the sensitivity of response to changes in temperature and moisture, if these differ in different savannas;
(e) root:shoot ratios;
(f) probable fire regime;

(g) potential animal production and herbivory;
(h) forage quality;
(i) deciduousness of the vegetation.

3.10. Potential links with IGBP. PAM and PAN studies at the various scales described should interface easily with a number of IGBP (International Geosphere, Biosphere Program) projects, but above all with the GCTE (Global Change and Terrestrial Ecosystems) program. In particular, the links are likely to be as follows:

1. At the regional, landscape and possibly catena scales: BAHC (Biospheric Aspects of the Hydrological Cycle), GCTE, GCEC (Global Change and Ecological Complexity), PAGES (Past Global Changes), GAIM (Global Analysis, Interpretation and Modelling) and RRCs (the IGBP Global Change Regional Research Centers).

2. At the patch and possibly catena scales: GCTE, GCEC AND PAGES.

In more general terms, at the catena scale and above, close links must be made with geomorphological processes, as well as with the meso- and macro-level climatic changes. At the scale of the catena and the patch, responses to PAM-PAN in a range of dependant variables may prove predictive of the overall direction of certain global changes, and will be significant in terms of the human use of the environment. The link with the GCTE should be especially highlighted in this respect. The objective of this project is "to develop the capability to predict the effects of changes in climate, atmospheric CO_2 and land use on terrestrial ecosystems, and how these effects can lead to feedbacks to the physical climate system." In as much as certain of these changes will be mediated through the PAM-PAN plane, savannas should exhibit short-term, identifiable shifts in certain of their dependent variables. Because one of the key tasks of the GCTE program is to predict changes in functional vegetation types, this must be regarded as an urgent task in the study of the world's savanna formations.

3.11. Quantifying the PAM-PAN Plane. General approach. RSSD scientists differ in their perceptions as to the best way to formulate the PAM and PAN axes. These perceptions constitute alternative hypotheses. To test these hypotheses we propose to compile minimum data sets for about 30 sites occupying the complete range of variations of moisture and nutrients in savannas. The data set will also include a number of vegetation characteristics. Participating scientists will then endeavor to predict the vegetation characteristics on the basis of their favored model or index of the PAM and PAN axes. A related question is whether integrative indices can be related to remotely sensed estimates of albedo and surface roughness thereby providing explanatory input into General Circulation Models (GCM). Detailed studies may need to be conducted at various savanna sites to determine if a minimal subset of easily obtainable variables can be used to generate a meaningful integrative index.

The results of the proposed compilation will be compared at a subsequent workshop, at which time it is hoped to develop an index incorporating the most discriminating features of the various models proposed to differentiate distinct savanna types and trends in structural characteristics.

The data will be entered into a common data base andmade available to participants on a disc. The required data are listed below and the format for the data will be drawn up by the coordinator (Dr. Bob Scholes; Department of Botany, University of the Witwatersrand, Private Bag 3, WITS 2050, Republic South Africa) who will distribute data to all RSSD members. Any scientist possessing a set of minimum data and wishing to participate is urged to get in touch with the coordinator.

Data templates will be distributed in late 1990 or early 1991. With the cooperation of participants the full data set can be compiled and distributed by mid 1991, so that participants will have a year to work-up the data for presentation at the PAM-PAN workshop planned for March 1992.

3.12. Minimum Data Sets

The basic information required for each site is:

A. Site characteristics (a site is a homogeneous study area at the patch scale):
1. latitude (degrees and minutes)
2. longitude(degrees and minutes)
3. elevation
4. parent material
5. aspect
6. slope
7. topographic position
8. history (e.g., bush control, grazing, fire and prior land use)

B. Soils data (if new data are to be collected it is suggested that the methods of the Tropical Soil Biology and Fertility handbook be used). For each distinct horizon down to the limit of rooting the following information is required to quantify the PAM axis:
1. bottom depth of the horizons
2. bulk density
3. sand, silt and clay content
4. the four cardinal water holding capacities: saturation (calculated according to a given formula using bulk density (BD/2.64); field capacity, wilting point(1.5 MPa); and residual(10 MPa). The last two can be calculated from texture and BD using the "Retfit" package. These values will be calculated by the data coordinator.
5. organic carbon (state the method)
6. percentage stone content (>2 mm). The nature of the material below the described soil profile needs to be specified (e.g., water table depth, lithic contact, or deep soil).

Validation of the daily water budget models requires a time series of the soil water contents by depth for some of the sites. To quantify the PAN axis the following additional information is required per horizon, with emphasis on the sub-soil horizons:

7. extractable Ca, Mg, K and Na;
8. exchangeable acidity in soils with pH < 5;

9. CEC and the pH at which it was determined;
10. extractable P by whatever method (state method) is appropriate at the site with an indication of the relative level (e.g., very low, low, medium, high and very high);
11. total N.

C. Climate

Time series data (for up to five years)
- (1) daily rainfall;
- (2) monthly mean maximum and minimum temperature over the same period.

Long term means (state number of years):
- (1) monthly rainfall;
- (2) monthly mean maximum and minimum temperature.

D. Vegetation.

Woody vegetation overall
- (1) total projected canopy cover by woody plants;
- (2) total density of individuals with a basal circumference greater than 10 cm;
- (3) total basal area of the plants greater than 10cm circumference.

For trees alone (defined as predominantly single stemmed woody plants > 2.5m), present data for up to 100 individuals:
- (1) height;
- (2) basal area (accumulated for trees with > 1 bole).

For shrubs (defined as predominantly multi-stemmed woody plants < 2.5 m high):
- (1) canopy volume (canopy depth x width 1 x width 2).

For the herbaceous layer:
- (1) peak standing crop (live and dead) for as many years as are available and the total rainfall for those years;
- (2) mean maximum height of the vegetative organs;
- (3) proportion of the peak biomass contributed by non grass plants;
- (4) proportion of the grass biomass contributed by annual species.

4. HIERARCHY THEORY AND THE GRASS-TREE INTERACTION

4.1. The grass-tree interaction and modelling: some initial considerations. The roots of many savanna trees are deeper than those of grasses (Sarmiento 1984). This deeper rooting depth of trees is supposed to allow trees to tap the water in the subsoil, thereby partitioning the soil water resource and reducing competition with grasses (Walker and Noy-Meir 1972). Deeper roots may also be necessary to keep the trees alive during droughts. Data on the actual distribution of roots of woody and herbaceous species are however few. The important data required are those which would allow the graphing of water extraction against depth in different savannas across the PAM-AN plane. Form and function are both implied in the expression "grass-tree interaction".

If trees, shrubs, and grasses are water limited, the relationship between these competing lifeforms can be represented graphically. When grass production is plotted against woody (tree and shrubs) leaf area (or surrogates such as basal area), a family of curves is obtained. In general they are non-linear, which implies the existence of a woody (tree-shrub)-grass interaction. It is suggested that these curves reflect different general conditions of the environment, specifically different levels of plant available moisture and available nutrients (i.e. position on the PAM-PAN plane).(Fig. 6).

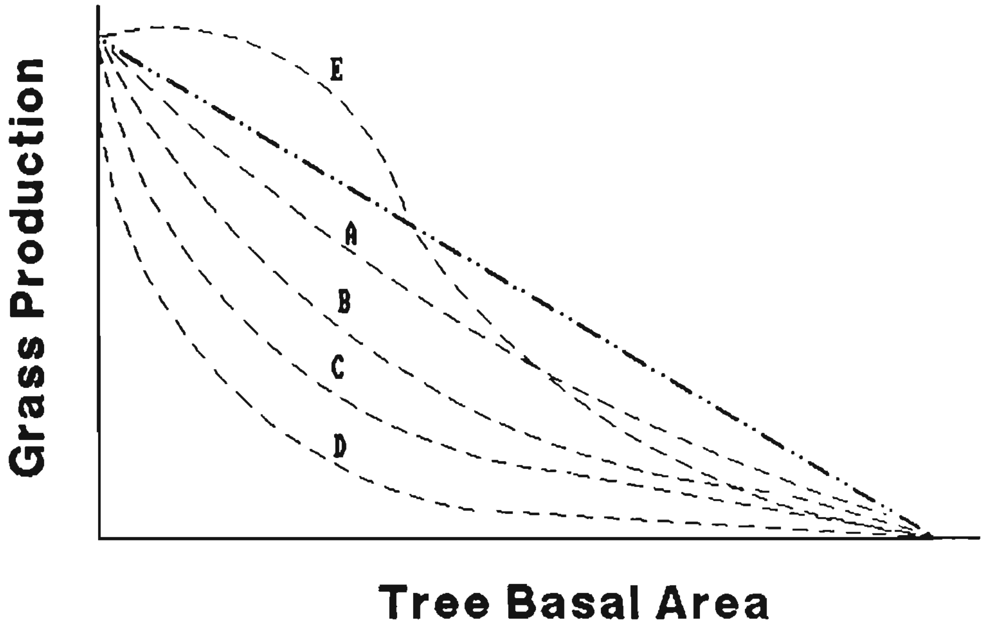


Figure 6. The family of curves representing the interaction between trees and grasses. A-D: increasing levels of interference; E: here at low to intermediate densities trees are beneficial to grass growth; at higher densities they reduce grass production.

The magnitude of the interaction between trees and grasses is also a function of the degree of clumping of the woody elements in a savanna. It is maximal where the trees are dispersed. Where the trees are highly aggregated, a savanna can be viewed as a mosaic of pure grassland and pure forest, and the woody-grass interaction is minimal.

In some locations, the distribution of rooting depths of trees and grasses overlap to a high degree, suggesting that partitioning of the two groups by this means is not a significant mechanism of niche separation (Figs. 7 & 8).

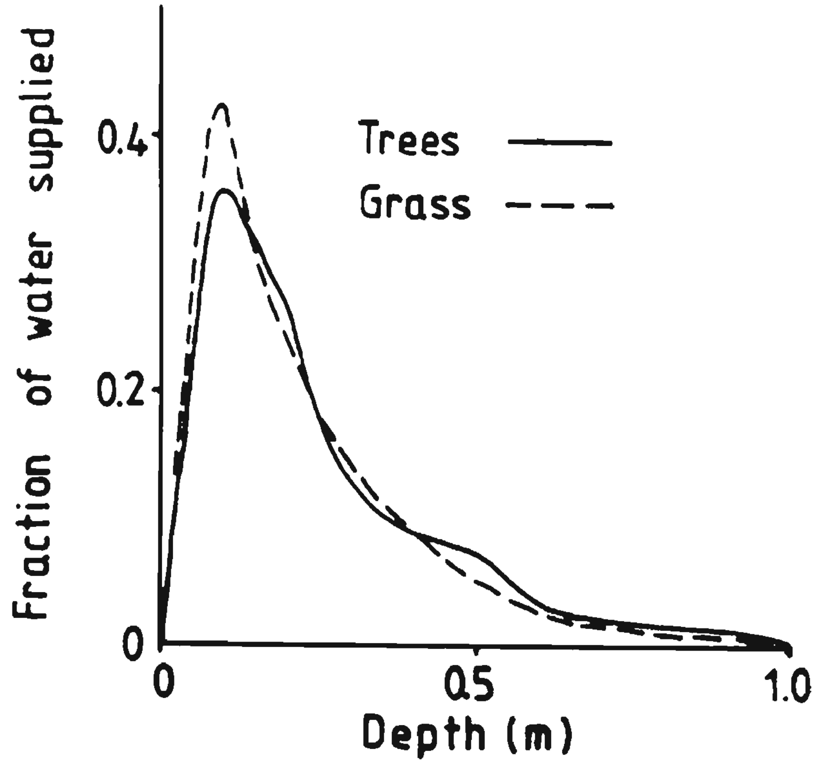


Figure 7. Niche separation between trees and grass on the basis of the depth of the soil layer from which they obtain their water supply. These results, obtained from a simulation study based on observed rooting patterns, soil hydrological characteristics and long-term real rainfall sequences from Nylsvley, South Africa, suggest that niche separation on the rooting depth axis is slight (unpublished data, R.J.Scholes, Dept. of Botany, Wits 2050 Rep. South Africa)

In many locations, the Leaf Area Index (LAI) for trees shows a longer period of high values than that for the grass layer. The trees have the reserves to begin growing before grasses and finish leaf growth after grasses. In such a case the tree and grass layers may be separating temporally their exploitation of resources. In West African savannas however, grasses begin production before trees (Menaut et al. 1990).

Grass production is usually related to distance to nearest tree or shrub (Donaldson and Kelk 1970; Walker, Moore and Robertson 1972; Beale 1973; Aucamp et al. 1983). Therefore, woody and tree layers may separate using the horizontal dimensions as well as (or rather than) the vertical. Woody (tree and shrub) species may be regulated by competition with other trees, while grasses may exist where tree-grass competition permits it. The level of clumping of trees (and shrubs) may also facilitate coexistence between tree (and shrubs) and grass layers. If all trees in an area are together in one corner then suppression of grass by trees would be minimal, perhaps negligible. Comparisons of such situations may allow the assessment of this interaction. It may be useful to examine the slopes of the curves of grass against tree production in relation to indices of tree clustering for the range of available sites.

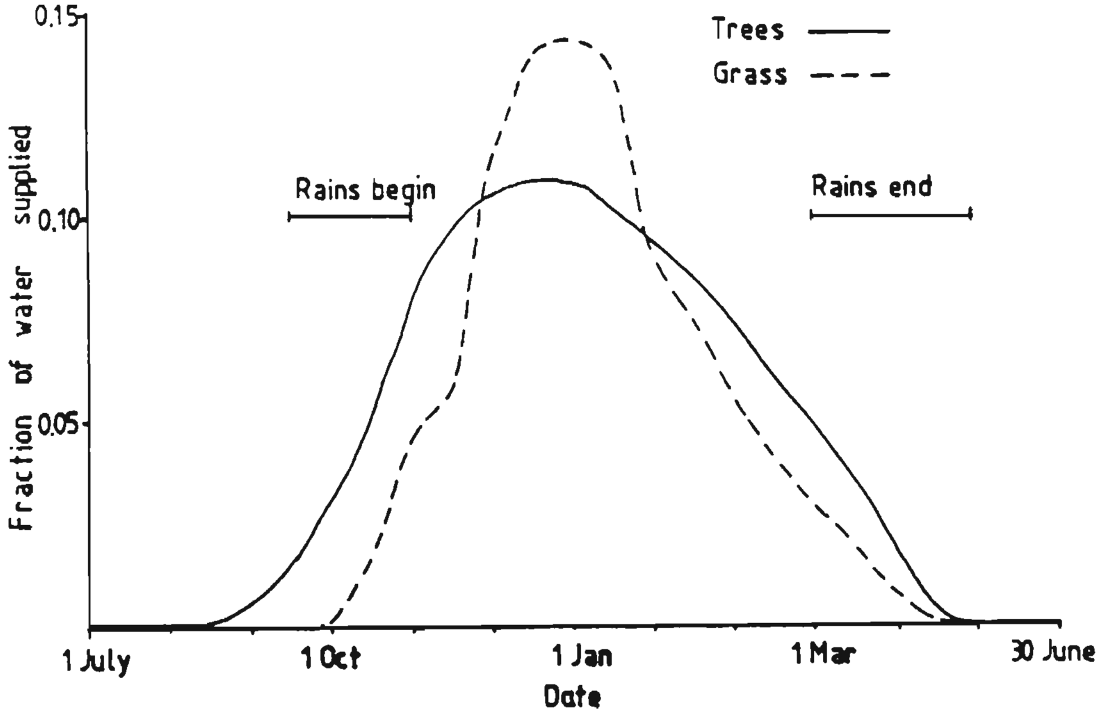


Figure 8. Niche separation between trees and grass on the basis of the time of the year at which water is used. The results are from the same simulation study as figure 7, which included observed data on the temporal pattern of leaf area development by trees and grass. Note that the separation on the temporal axis is more convincing than that on the rooting-depth axis (unpublished data, R. J. Scholes, Dept. of Botany, Wits 2050 Rep. of South Africa).

In some cases the tree impact on grass may be positive. For example, at Turkana (Kenya) where the savannas are at the dry end of the spectrum, shading of grasses can increase their production and survival by decreasing water loss.

Grass production may dominate that of trees when the trees are juveniles. This means the interaction changes with time facilitating coexistence. In other words, competition in savannas is markedly asymmetrical, and the direction of the asymmetry changes as trees mature. There is experimental evidence of the effect of the removal of grass on shrub production in an African study (Walker, Moore & Robertson 1972; Beale 1973; Knoop & Walker 1985).

Event-driven systems need frequent, strong and varying disturbances to drive them away from an equilibrium point. Year-to-year variation in rainfall is important for the maintenance of savannas. Primary production of both tree and grass layers varies in response to the considerable year-to-year rainfall variation experienced in savannas. This results in opportunities for temporal partitioning between the two groups as grasses recover from drought more quickly than do trees. In deep sandy soils (e.g. Kalahari sands in southern Africa), there is great difference in rooting depths between trees and grasses.

Different processes can be involved in the effect of tree on grass (e.g., shading) and of grass on tree (e.g., moisture restriction). Furthermore, the same process (e.g., shading) can have different outcomes depending on other factors. Plant Available Moisture is more than a single axis. It is necessary to separate top- and sub-soil layers in examining the influence of PAM on production.

Sometimes a successional pattern is observed. Early tree species in a succession might exhibit one pattern of rooting (e.g. deep), while a later-appearing species might exhibit another pattern (e.g. shallow). Initially grasses may be enhanced by trees but later deciduous trees may shade out grasses (Archer 1990). It is also important to consider different sorts of trees including, top soil trees, deciduous trees, nitrogen-fixing trees, etc. (Smith & Walker 1983).

The fire regime may change the rate of change but not its general direction. Nevertheless, individual competition is more important than fire (Menaut et al. 1990). In many arid and semi-arid savannas, if fire is excluded, trees first increase then decrease, so that fire is not necessary to maintain the savanna (B. H. Walker personal observation of the 40 year protection blocks at the Matapos Research Station in Zimbabwe; Walker 1981).

Topographic variation is likely to be more important in determining point moisture input than rainfall. In this respect, big rainfall events are of great importance as the allow lateral movement of rainwater creating run-off and run-on areas. Patch formation is closely related to the pattern of run-off/run-on areas (Pickup 1985, 1991; Tongway & Ludwig 1990).

Soil texture information is essential for modelling savanna production. The compilation of a list of detailed examples of soil and vegetation would be useful in separating the important from the unimportant factors for understanding the flux of trees through time.

Comparative tree seedling rates across different savanna systems are also needed. Some tree species mainly reproduce asexually and dominate on some sites.

There is a need to incorporate the influence of animals (e.g. termites, granivorous birds) on pattern formation. Termites create small local nutrient patches which are utilized by different components of the vegetation and thus may facilitate small-scale partitioning of grass and tree layers. Differential mobility of different nutrient ions can occur if overgrazing of grass layer allows. This may permit establishment of thickets. Grazing may decrease root extension and change the competitive interaction between the tree and grass layers.

A number of different conditions can produce savanna (e.g. demography, position on PAM-PAN plane). It is important to model at the landscape scale as well as the patch scale. At the catena level, there are clear influences of overgrazing and other factors on run-off and run-on areas which it will be necessary and feasible to model. The wider time scale should also be considered. Not only events but cycles and trends should be considered.

While simulation models are often restrictive, it is possible to model all the hypotheses mentioned above. However, it is necessary to specify the entire system for simulation models to work. Further, under some conditions (growth rate $r>1$) models are not going to tell us much about the grass/tree interaction. The best way to proceed may be to explore alternatives using computer models. A generalized model could be constructed using the model structures currently available. The models, which would need to operate at several scales, would be useful to understand the impact of future climate changes.

A theoretically neutral model shell is required as a starting basis which then has new features added as required. With a large area and complex rules, the computational load would be huge. It is essential to keep the rules as simple as possible without losing essential features.

4.2. Shrubs in Savannas. Deliberations on the grass/tree interactions in savannas should be expanded to include the shrub component where applicable. Savannas dominated by shrubs rather than trees include (but are not limited to) the *campo sujo* in *cerrado* (Brazil), the *Acacia* savannas of Australia, the *Prosopis-Acacia* savannas of southern Texas and northern Mexico, and the Turkana region of Africa. Relative to trees and grasses, shrubs exploit space above ground and below ground (potentially) differently. As such, savanna models should distinguish between trees and shrubs and be able to accommodate situations where shrub abundance may change in response to biotic and abiotic factors and disturbance. For example, the proportionate contribution of shrubs relative to other lifeforms in savannas may be mediated by herbivores. Browsers may reduce shrub abundance or shift shrub composition to unpalatable species. In other cases, certain levels of grazing on grasses may contribute to an increase in shrub abundance.

The shrub designation encompasses a range of growth forms. Although shrubs are typically defined as multistemmed woody plants less than 2 meters in height, they span a range of "woodiness" and stature ranging from dwarf, suffruticose herb-like plants to tree-like plants exceeding 5 meters height. The range of growth form expression within a genus may vary substantially depending on environment. Environmental conditions and disturbance will also influence the relative contribution of trees and shrubs to savanna structure. Trees, with their potential to achieve substantial vertical stature relative to other lifeforms, are potentially suited to compete effectively for light, develop large canopies for light interception, escape ground-dwelling herbivores and elevate meristems above flame scorch heights. The "costs" associated with this approach, relative to other lifeforms, is a substantial expenditure of energy (respiration) and nutrients in non-productive tissue and the requirement of large amounts of water to meet transpirational demands. Shrubs represent a scaled-down version of the tree lifeform that may be better suited to environments where water, nutrients and/or light are more limiting. Shrubs, with their multi-stemmed habit, have a flexible canopy architecture that can be advantageous in variable and extreme environments and allow them to: (1) cope potentially better than trees in stressful environments and/or environments subject to periodic disturbances associated with drought, freezing, fire, etc.; (2) dominate mid-seral stages in forest succession in savanna-forest transition zones; and (3) co-exist with trees. The ability of many shrub species to regenerate vegetatively from roots or other substantial underground structures (crowns, burls, lignotubers, etc.) facilitates both persistence and the exploitation of horizontal space. The capacity for some species to develop extensive lateral and/or deep tap root systems are potentially adaptive in environments where soil resources are heterogeneously distributed. Shrubs in some families (Leguminoceae, Rhamnaceae, Rosaceae, and others) have the capacity to form relationships with nitrogen-fixing bacteria (*Rhizobium*) or actinomycetes (*Frankia*). These various attributes also make shrubs an important component of landscape restoration programs in savannas. As a group, shrubs provide herbivores with a better source of protein, carotene and phosphorus than grasses, both in terms of concentrations and seasonal availability. However, high fiber contents and, in many species, high levels of secondary compounds will influence nutritional value to consumers.

4.3. A Hierarchical Approach to the Determinants of Savannas. At its inception, RSSD proposed four main determinants of savanna functional characteristics (Frost et al. 1986):

Plant Available Moisture (PAM)
Plant Available Nutrients (PAN)
Fire
Herbivory

PAM and PAN were regarded as the primary determinants of savanna functioning, leading to the concept of a PAM-PAN plane intended "to produce a classification of the world's savannas based upon an ordination of actual sites in relation to these two indices" (Frost et al., 1986).

Such a direct ordination implies that the two axes (PAM and PAN) are orthogonal (i.e. not correlated) and may vary independently and are of equal importance. This is, of course, only an assumption, and it is possible that the importance of PAM and PAN may vary in different savannas and at different spatial and temporal scales (as inferred in Fig. 1). In particular, as RSSD has progressed, it has been suggested that PAN may be a subordinate determinant to PAM (3.3.).

Alternatives to direct ordination of sites on the PAM-PAN plane are, for example, indirect (or derived) ordination (such as principal components analysis [PCA]) and 'hierarchy theory' (Allen and Starr 1982; O'Neill et al., 1986). Thus, a PCA of a matrix of sites x environmental variables might show that one factor may account for most of the variance in the data. Such a factor might be interpreted as a single environmental variable (such as soil water potential), or might be interpreted as a complex of several variables and/or site characteristics (e.g. PAN or PAM).

It is only possible to perform an indirect ordination (such as PCA) when a sufficient number and distributional range of sites have had a minimum set of environmental variables quantitatively determined (3.11). There would also be the problem of scale; would the variables be averaged for a region of the world's surface (a savanna type) or for many sites within and between geographical distributions of savannas? At least with the PAM-PAN plane, sites can be ordinated as data on PAM and PAN become available. However, even then the problem of scale must be addressed.

The approach of 'hierarchy theory' allows a consideration of the relative importance of the main determinants of savanna function and of spatial scales. There are, however, a number of problems with 'hierarchy theory' which must not be overlooked in its application to the analysis of the determinants of savannas. The first is that to date, the protagonists of the theory have not delimited any hierarchy generative strategies. Here, as an alternative approach to the goal of producing a description of savanna functioning (and an eventual classification), it is used simply as a conceptual tool, not as a clearly stated theory. The hierarchies presented in Figs. 9 and 10 are derived from collective reasoning based upon ecological expertise rather than available site data.

In producing the hierarchies, certain tenets of hierarchy 'theory' have been adhered to:

At each level of a hierarchy there are one or more holons. Holons represent subsystems which, at the same level of the hierarchy, interact frequently and strongly. Holons at different levels of the hierarchy have different process rates. As a result, any measure suggested for collecting data about a holon must be a measure of the rate of a process.

As one moves up the hierarchy, rates of processes become slower (which relates to the temporal response scale of Fig. 1).

Holons at one level in the hierarchy are constrained by those above. As such, a hierarchy of determinants exists within the system being studied or modelled. If the four presumed major determinants of savannas (PAM, PAN, fire and herbivory) were ultimately reasoned to be independent and of equal importance, they would be represented as four holons at a single level in a one layer 'hierarchy'. In fact, this was reasoned not to be the case, as shown in Fig. 9.

In addition to a hierarchy of determinants, it was also reasoned that a determinant process may operate differently (or not at all), not only in rate but also in effects, at a different spatial scale. Thus, in the hierarchy of determinants, each holon may be decomposed into an internal hierarchy determined by spatial scale (Figs. 9 and 10).

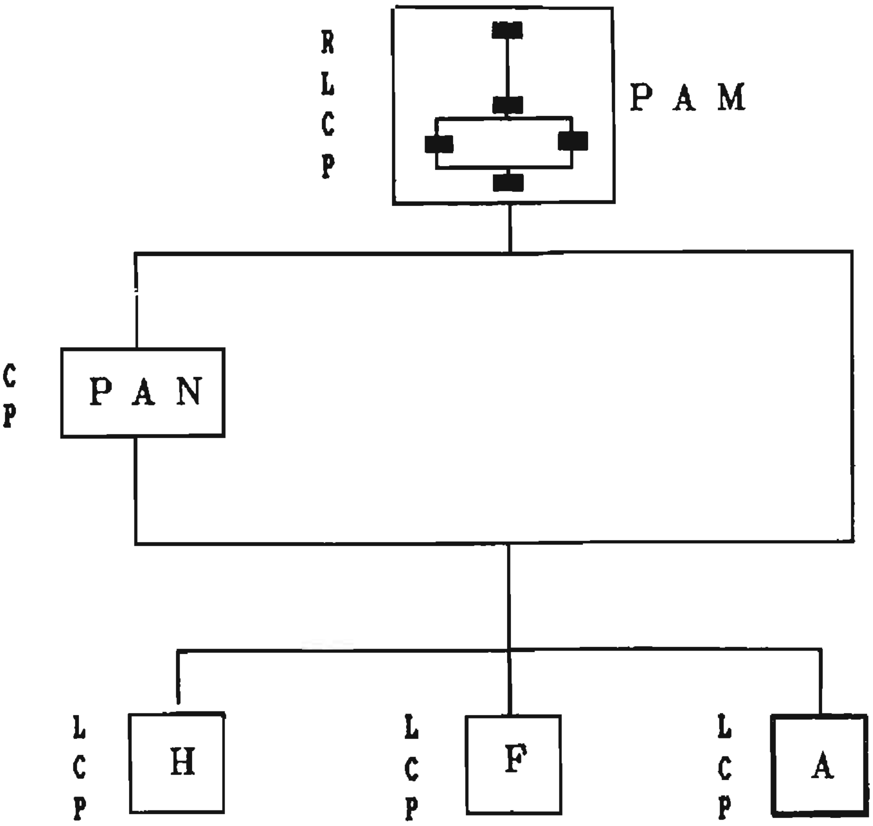


Figure 9. Hypothetical hierarchy of savanna determinants. PAM = Plant Available Moisture; PAN = Plant Available Nutrients; H = Herbivory; F = Fire; A = Anthropogenic factors; R = region; L = landscape; C = catena; P = patch. More details in text.

4.4. The two core diagrams. The two core diagrams (Figs. 9 and 10) illustrate possible non-nested, ecological hierarchies; one showing the overall hierarchy of constraints and processes for savanna formations, the other the internal constraints affecting PAM in particular. Similar diagrams to the latter can also be constructed for the other holons; PAN, Herbivory, Fire and Anthropogenic factors. However, their internal structures are not as easy to define as that for PAM, and advice from social scientists and anthropologists would need to be taken to analyze the internal workings of the Anthropogenic Factors holon, which we here leave as a "black box."

It will at once be noted that the hierarchies presented exhibit a number of key characteristics.

They are spatially scaled against the letters P, C, L, and R, standing for the main scales of savanna study, namely the patch, the catena, the landscape, and the region. These levels were recognized as vital in understanding the functioning of savannas and of PAM in the report of the relative importance of PAM and PAN presented in section 3.

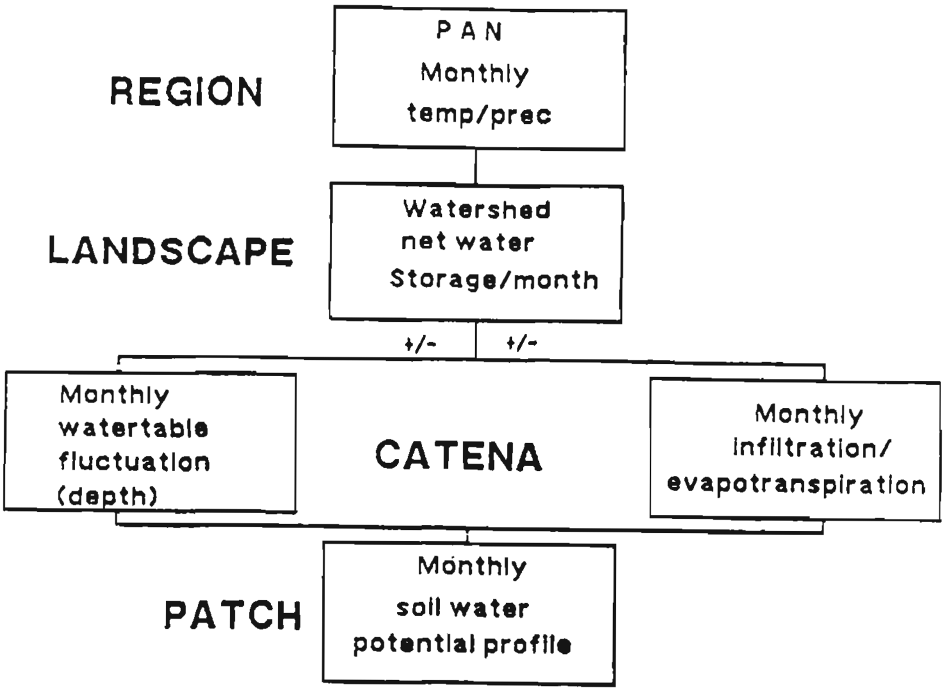


Figure 10. Key measurable PAM variables at the region, landscape, catena, and patch, that will enable savanna studies to be slotted easily into other studies, e.g. via geomorphology and hydrology, which employ the same variable as a key part of their studies. At the catena level (C), we think two possible determinants are required, which in some savannas will work together, whereas in others only one variable will apply.

In the PAM hierarchy , the influence of PAM is seen as mediated through a key measurable variable or variables, often compound in character, which will also enable savanna studies *per se* to be slotted easily into other studies, e.g. via geomorphology and hydrology, which employ the same variable as a key part of their studies. We are not completely wedded to the variables here suggested and further attention will need to be given to their refinement and choice.

At the catena level (C), we think two possible determinants are required, which in some savannas will work together, whereas in others only one variable will apply.

Likewise, in the full savanna hierarchy, the influence of PAN may be bypassed in many savannas, hence the pathway linking PAM directly with the third level.

Throughout, processes are constrained by the higher levels of the hierarchy, so that processes move up the diagram and the constraints move down. At any given hierarchical level, such as a patch or a catena, Herbivory (H), Fire (F), and Anthropogenic (A) processes will take place freely. That is, they may influence each other in unlike ways in different hierarchical relations.

The strengths of the above approach may be summarized as follows.

The system is organized in a logically structured way which places relative values on the importance of the different holons.

PAN is clearly shown to be of secondary importance to PAM, and not always of significance.

The system forces the generator to identify a key measure(s) through which PAM, PAN, etc. is mediated at any given level of the hierarchy.

It is essentially an aid to analytical thought.

4.5. Rare Catastrophic Events (History). The major types of rare catastrophic events, such as severe droughts, intense fires, frosts, outbreaks of insects, and major human interventions, represent extreme conditions of variables already identified as important input variables at one or more of the scales considered. It is arguable, however, that it is appropriate to establish a special holon for catastrophic events as there are certain types which are unrelated to the previously recognized variables and holons. Also, both from a logistic and a conceptual point of view, it might be preferable to treat historical events as a separate box while modelling its effect on top of the pattern maintained by other processes.

Historical events might act at all scales considered, but are increasingly important at small scales. It is not clear at what position relative to the other holons in the hierarchical system proposed it should be considered. Given its long term frequency, it should probably be considered at the top of the hierarchy. In fact, the modelling of the effects of rare events should be central to both RSSD and IGBP objectives.

5. APPROACHES TO MODELLING SAVANNAS

5.1. Introduction. The proposed modelling effort will comprise three main approaches, each of which characterizes a different level of complexity.

Individual plant models: such models are spatially explicit, interactive, explanatory models which address changes in plant growth and composition at a point, from which changes in structure, demography and competition within a patch are simulated.

Large-scale process-response models: such models have been designed to address interactive processes occurring at a landscape or regional scale, often in the context of guiding or supporting management decisions. Examples of such models include STEP (South Turkana Ecosystem Project), PYRO (a decision support model for fire management) and SEESAW (Socio-Economy and Ecology of Semi-Arid Woodlands).

Ecosystem production models: such models are largely predictive with outputs which can serve as inputs to global climate models. The models do not explicitly consider individuals although a model such as CENTURY can be reduced to the scale of a single tree and associated grass, and thereby can potentially be linked to individual plant models.

The development of new models is considered to be impractical at this stage in the program. A more realistic approach is to seek to integrate existing models, with appropriate modifications and additions, into one or more general models. The concept of a generic savanna model is also untenable, given the variety of purposes for which the models are needed.

The question of scale in modelling is particularly important in the context of savanna dynamics. Fig. 11 shows the relationships between different classes of models within savannas, together with the appropriate spatial and temporal scales of the included processes. The wide spatial and temporal scales covered by the models is obvious. It needs to be tested whether the output from models which simulate processes operating at fine spatial and temporal scales can be legitimately extrapolated to larger scales in heterogeneous systems such as savannas.

Some of the more general or potentially more widely applicable models are described briefly below. Most are simulation models, although one analytical model designed to investigate the basis of grass/woody plant interactions is described.

5.2. Some Existing Models with Applications to Savannas

5.2.1. An Analytical Model of Grass-Woody Plant Interactions (Brian Walker and Imanuel Noy-Meir). This model was developed to test the hypothesis, first proposed by Walter, that the coexistence of woody plants (W) and grass (G) is a consequence of their separate use of the topsoil (T) and subsoil (S) moisture (where T and S are the total annual amounts of water in the

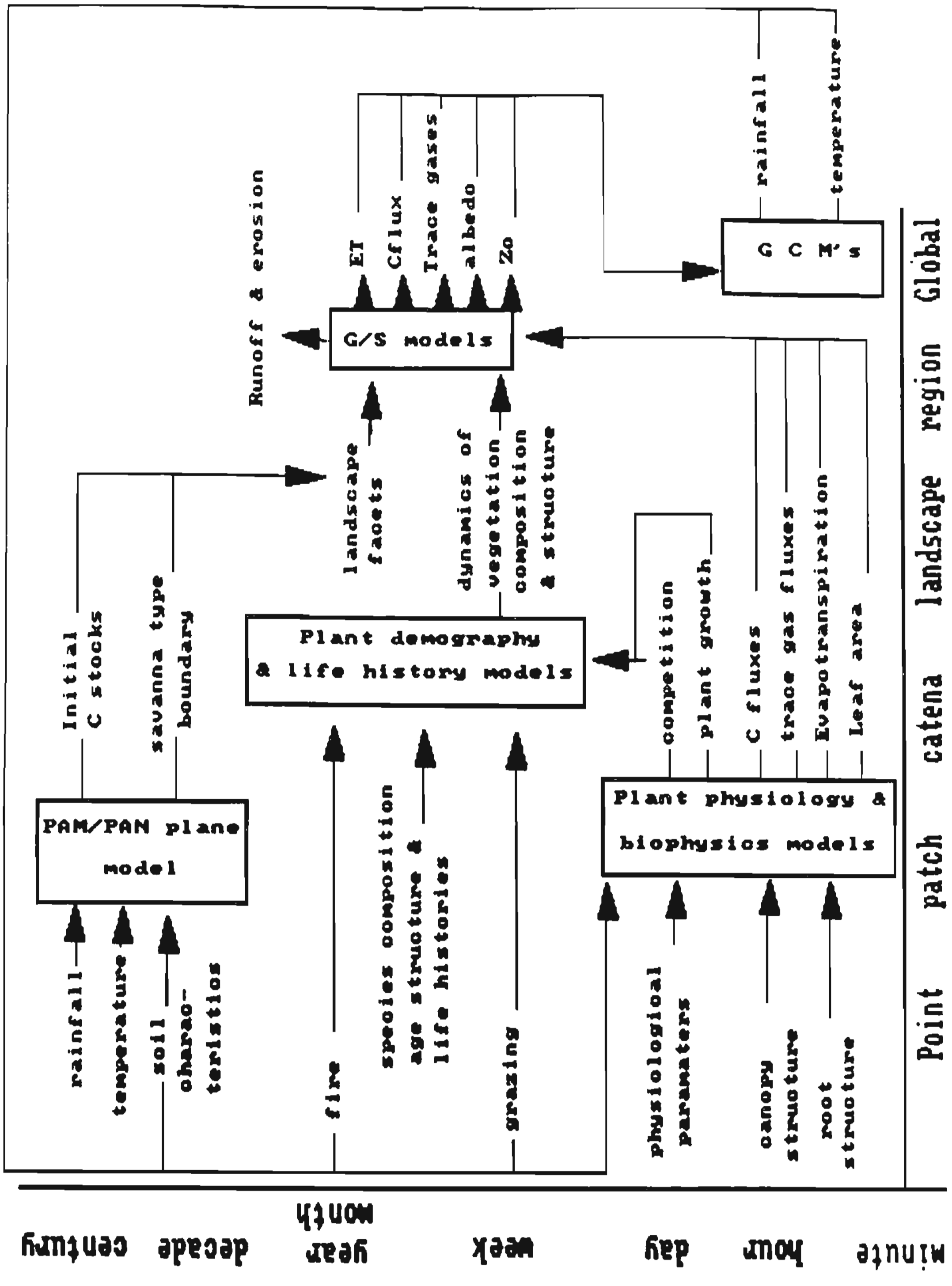


Figure 11. The relationships between different classes of models within savannas, together with the appropriate spatial and temporal scales of the included processes, and outputs.

top and subsoil layers). The model is based on equations for changing water content in topsoil and subsoil through parameters for uptake by grass (only from topsoil) and woody plants (from both topsoil and subsoil), and for converting water uptake to biomass. Water infiltration declines at low grass because of soil capping (depending on soil texture), thereby lowering the soil content in topsoil, whereas direct addition of moisture to subsoil is largely a function of the concentration, through stem flow, and rapid infiltration of rainfall at the base of woody plants.

The model is sensitive to the proportional uptake of water by grass and woody plants from topsoil and subsoil, and to the two infiltration parameters. Depending on these values, the isoclines for equilibrium values of grass and woody plants indicate that the system can have a single, stable, joint equilibrium (high woody and low grass - essentially a woodland on sandy soils) or three equilibrium states: two stable equilibria (high grass and low woody, or woody alone [thicket]), separated by a joint, unstable equilibrium of intermediate grass and woody plants. As the root distributions of grass and woody plants become more similar, so the isoclines converge and little change (pressure) is needed to move the system to or beyond the unstable state.

The obvious limitation of the model is its assumption of equilibrium conditions. Although such an equilibrium is never attained in a savanna because of a highly variable climate, the model provides a rapid, useful and easily interpretable view of equilibrium behavior in savannas under a wide range of climatic conditions.

5.2.2. VEGOMAT (Hank Shugart and others). The VEGOMAT model (presented by Smith et al. and Burton et al. at the 1989 meeting of the Society of Vegetation Scientists in Uppsala) is a general purpose vegetation simulator intended for multiple life-form interactions. The model simulates the birth, growth, and mortality of individual plants (grasses, shrubs, and trees) at biweekly time steps for a set of nested quadrats of different size. The smallest quadrats are 1 x 1 m, on which the growth and fate of plants less than 1 m high are simulated. Larger plants over a given plot are allowed to shade, extract water, and use nutrients from a given small plot. Plants that grow taller than 1 m in a given year are 'promoted' to the next size quadrats (5 x 5 m) by computing the mean and variance of 'promotable' individual plants and drawing from this distribution new plants to plant in the layer. Plants that grow to a larger size on the 2nd level plots (typically shrubs or small trees) are promoted likewise to the third computational unit. The model essentially computes the grass, shrub and tree layers and uses the smaller quadrats to compute the recruitment of trees and shrubs.

The model is designed to interface with the CENTURY model (see below) for nutritional reserves on the quadrats. A Priestly-Taylor evapotranspiration model (requiring daily air temperature and radiation input) is used to compute the water balance. The water-use of each plant is determined by its current leaf area index. The soil is divided into three layers with the shallow layer associated only with the smallest plots; the two top layers associated with the intermediate size plots, and so on for the larger plot that interacts with all three layers.

The model is designed for investigations of the grass-tree interactions on the North American Prairie-Forest border (which can have a savanna-like character, particularly along the southern border). It has also been used to simulate old-field succession (in which the replacement of grasses by shrubs by trees occurs over a time sequence). The model is largely under development at present and is therefore likely to be modified. The model is available on a case basis for any number of applications and there is particular interest in seeing it applied to savannas.

5.2.3. FATE (Ian Noble and Andrew Moore). FATE simulates a small homogeneous patch of the landscape (see below for alternative versions). It uses a time step of a season or year to simulate the dynamics of cohorts of species or functional groups for time spans of up to many centuries. The model is written in TURBO PASCAL and runs on a standard PC. A 'C' version of the core of the model is available. No special graphics are required.

FATE uses a qualitative one-sided competition model for a unidirectional single set of resources (or several correlated ones). The entities interact across multiple strata. Seed pools are followed through time with simulated germination and establishment responding to a qualitative, resource-sensitive model. The impact of disturbance is included.

Approximately 30 to 50 parameter values are required from the user (depending on the number, intensities and types of disturbance). These are entered in a simple spreadsheet form with context sensitive help. An expert system is being written to guide users through this process. FATE can usually be parameterized using the empirical knowledge of an experienced field biologists.

The principal application of FATE is to questions of the long-term management of disturbance-prone systems (e.g.,. in management systems with prescribed and wild fires). A special version is available for the Kakadu woodlands in northern Australia and another is under development for Australian semi-arid woodlands. The standard version, with examples, is available as both source and EXE files from Ian Noble.

FATE simulates 100-500 years/sec on a 12 Mhz AT. Thus it is feasible to link many cells together to create a landscape. Hooks for the transfer of material (e.g., seeds) and the spread of disturbance can be provided.

Moore and Noble have also developed software that creates a semi-Markov version of a specific FATE parameterization that produces output indistinguishable from FATE within bounds specified by the user (including a time horizon - e.g., no simulations will run beyond 150 years). This reduces the running time of the model to a simple 'look-up' process in the computer, thereby achieving simulation speeds 1000 to 10,000 times greater than that of the original model. The semi-Markov version can be added to a GIS to create an extra layer conveying information about changes through time, or it can be used to describe large landscapes. Collaboration with other scientists to develop new landscape versions of FATE is welcome.

5.2.4. MUSE (Ian Noble, Carlos Prado and Jean-Claude Menaut). MUSE simulates a spatial 'grid' of variable size (e.g., 10 x 10 to 1000 x 1000 m) in which individual trees are treated as objects at precise locations within the overall space. It uses a daily to monthly time step within which changes in the establishment, growth, reproduction and mortality of individual trees, grass and forbs in each grid cell can be simulated for periods up to decades. Any number of species/functional groups can be included.

MUSE is a 'shell' in that it provides the basic code to handle the geometry of a 3-D interacting forest, savanna or shrubland. It provides default code for the major modules. These default modules deal with multi-strata interactions both above- and below-ground (no limits are placed on the number of strata except those imposed by processing time). The principal application of the model is one of testing hypotheses about plant dynamics.

The default light model provides a simple light extinction calculation suitable for use in photosynthetic response. The soil model uses a simple soil moisture budget and root distribution/activity to calculate water uptake. There is a plan to add CENTURY as a below ground nutrient module.

All of the essential features (e.g., those describing root uptake or root activity) are available as a series of user-modifiable functions. Carbon allocation is available as a constant allocation to various strata, or as a variable allocation based either on user-defined rules or one which allocates carbon to the 'most useful' strata. Seed dispersal from parent trees is simulated as input to precise locations in a spatial matrix. A simple degree-day germination and establishment model is provided as the default.

The range of parameters which must be specified depends greatly on the options chosen by the user. Essentially a light-, water-, nutrient- driven tree and grass model is needed. Interactions come about through resource depletion.

MUSE runs on a standard PC (a co-processor is a great benefit) using TURBO-PASCAL. It is likely to be translated to ANSI-C. The model is self-contained for graphics (EGA/VGA is preferred). Preliminary versions are running. Test versions should be available to researchers in the RSSD program in early 1991.

5.2.5. <u>SAVANNA</u> (Bob Scholes). SAVANNA is a point model of hydrology and primary production in a mixed tree/grass community. An early version of the model is described in a Ph. D. thesis (Scholes, 1987) but it is still under active development.

The model requires the following physiological data for each life form:
- specific leaf area;
- maximum photosynthetic rate;
- quantum efficiency;
- maximum transpiration rate; and
- root vertical distribution.

Associated soil data includes bulk density, stone content, and soil water content at field capacity, at the wilting point, and when air-dry, all by soil horizon. The model is driven by daily rainfall, maximum and minimum temperatures, to produce a detailed water balance, overlaps between plants in water-use, and plant production components on a daily, annual or long-term basis.

Future developments include a generalization of the model to consider any number of species or functional groups of plants (for example, the inclusion of shrubs); the incorporation of nitrogen cycling; and the elaboration of the point model to a patch model in which under-canopy and between-canopy areas are differentiated.

Limitations of the model include a poor representation of run-off and run-on; no consideration of plant demography; and semi-empirical rather than fully mechanistic representations of physiological processes.

5.2.6. STEP (Mike Coughenour, Dave Swift and Jim Ellis). STEP is based on a series of narrower but higher resolution models previously constructed by Coughenour and Swift. Each sub-model was constructed to fulfill various needs for the South Turkana Ecosystem Project (STEP). STEP is a regional, spatially explicit, model which is superimposed on a Geographic Information System (GIS). Current GIS data layers include a DEM (topography); mapped rainfall; surface water distribution; and a static plant biomass map derived from multi-spectral scanner imagery and 8 years of Normalized Difference Vegetation Index (NDVI) data using AVHRR. The simulation model is driven by daily rainfall; the NOAA GAC NDVI data are used for rough validation of the NPP model output. STEP operates at different time steps depending on the season. During the rainy season it operates on a daily time step; during the dry season the time step is extended.

The objectives of the model include tracing the biomass dynamics of trees and herbaceous plants; utilization of forage by livestock; livestock production (milk); and how these vary over time in relation to rainfall and drought.

The six sub-models which are incorporated in STEP include:

1. A primary production model which includes some elements of the GRASS model developed by Coughenour.
2. A catena model designed to account for run-on, run-off and general hydrological characteristics of the ecosystem.
3. A simple tree growth model designed to accommodate changes in woody cover over time.
4. A livestock energy and nitrogen balance model modified to also estimate livestock production and demography.
5. A human decision model which influences peoples' food intake, diet composition, and nutritional state. The model also influences livestock herd size through decisions about sales and slaughter.
6. Elements of a Drought Response Model developed earlier to examine the effects of single-year and multi-year droughts on livestock and human pastoral dynamics, is currently being incorporated into STEP. The model links the submodels on livestock population dynamics (submodel 4 above) and human decision-making (submodel 5) with a simple GIS forage production model to simulate the responses of plants, livestock and people to drought.

5.2.7. PYRO (Mike Mentis). This is a decision support model designed to assist savanna park managers in relation to the management of wildfires and two types of applied fire: security burns to protect people and property; and standard burns to maintain biotic diversity. The model is coupled to a geographic information system which is updated regularly.

The model has been designed, in terms of requirements for user expertise, hardware and software, to be within the reach of most park managers. The model has been written into a VP-EXPERT shell and uses Lotus 1-2-3 worksheets for the GIS; other worksheets or D-Base are also suitable. The model runs on an IBM-compatible PC-XT with a 20 Mb hard disk and printer. A print-out of every consultation is provided.

The required data include forecasted maximum wind speed and minimum relative humidity for the following day or two. The GIS comprises a grid overlaid on the park, with a record of when each grid cell was last burnt. The GIS must be updated manually.

The knowledge-base uses backward chaining and places priority on security burns over standard burns. Security burns are advised for as long as the system is incomplete, as defined in the GIS, and the fire hazard is below a defined threshold. Standard burns are advised subject to the completion of security burns, below a threshold fire hazard, and if the fraction of the park burnt in the current season is below that defined by park policy. Ignition points for standard burns are randomly selected (but tested for appropriateness in the GIS first). Advice on the management response to wildfires (either to leave or to extinguish) depends on the fraction of the park burnt to date within the season, and on the fire hazard rating.

The model is currently operational but has not been extensively tested. It is transportable and is aimed at providing a conceptual basis for decision-making; it can be readily modified to suit particular circumstances. The key features of the model are that it is economical in terms of hardware and software, and the program can be modified by persons of no more than modest expertise with computers. Advice is given rapidly; for wildfires, advice is given in less than 4 minutes (from boot-up).

The use of this model for deciding on standard burns ensures consistent application of park policy on burning to maintain spatio-temporal diversity. By reducing the arbitrariness of decision-making, the model enables park managers to get away from 'gardening'. Potential users of the model can obtain the knowledge-base and schematic GIS from Mike Mentis but they must acquire their own copies of VP-EXPERT and Lotus 1-2-3.

5.2.8. CENTURY (Bill Parton and others). CENTURY was originally a model to simulate the dynamics of C, N, P, and S in cultivated and uncultivated grassland soils. It has been subsequently adapted to simulate the dynamics of the same nutrients in forest soils. The savanna version of CENTURY amalgamates elements of both of these models with consideration of tree-grass interactions.

The model contains five submodels: a soil and decomposition submodel comprising three soil organic matter (SOM) fractions which differ in their rate of decomposition, itself a function of moisture, temperature, and carbon and lignin contents; a plant submodel which simulates the dynamics of nutrients in live and dead above ground material, live roots, and structural and metabolic surface and soil residue pools, as functions of precipitation modified by nutrient availability; and submodels for simulating N, P, and S dynamics. The model runs on a monthly time-step and can simulate the dynamics of soil organic matter over long time periods (100 to 10,000 years).

Regional trends in soil organic matter (SOM) have been successfully predicted using four site-specific variables: temperature, moisture, soil texture, and plant lignin content. Nitrogen input must also be known. The model has been used to simulate the process of soil formation; the effects of climatic gradients on productivity and the dynamics of oil organic matter; and the impact of cultivation on soil organic matter dynamics, nutrient mineralization, and plant production. The model has been validated by comparing the output from the model with observed data from sites in the northern Great Plains of the USA. The model correctly predicted the primary limiting nutrients for plant production and simulated the response of the system to the addition of inorganic fertilizer. The impact of grazing has also been simulated and has shown that steady-state levels of soil C and N are sensitive to grazing, and decrease with increased grazing pressure (Parton et al., 1987; Parton, Stewart and Cole, 1988).

6. RSSD AND GLOBAL CHANGE: HIGHER ORDER INTERACTIONS

Global climate change is predicted to alter the patterns of precipitation, temperature, evaporation, etc., in savannas. Just how the vegetation components of savannas respond to these changes is clearly a central issue within RSSD. Equally important questions remain to be asked, however, about the effects of these changes in turn on secondary production, land use, and microeconomic decisions taken by the people living in savannas; how possible changes in macroeconomic policies of governments, induced by changes in savannas and elsewhere, will create opportunities for, or constrain the actions of, savanna inhabitants; and how all these in turn might feedback to affect outputs to global climate. From 21-25 of January 1991 an RSSD conference-workshop on Economic forces and Savanna Land Use took place in Nairobi, Kenya, where the macroeconomic issues were discussed in detail. Here we focus on the relationship between climatic change and savanna land use. These scenarios are presented to show some of the possible direct and indirect effects of certain actions.

6.1. Induced Changes in Secondary Production, Land Use and Microeconomics. Some of the potential effects of climate change on secondary production, land use and microeconomics can be illustrated by considering two scenarios (Fig. 12).

Consider now the scenarios depicted in Fig. 12 in the context of a change in rainfall. Such a change could include (associated changes in temperature, evaporation, etc. are implied):

1. Changes in annual average amounts of rainfall.

2. Changes in rainfall variability affecting:
    - a) seasonality (i.e., longer dry seasons);
    - b) greater or lesser inter-annual variance;
    - c) the frequency of extreme events such as droughts, floods, frosts, or fires.

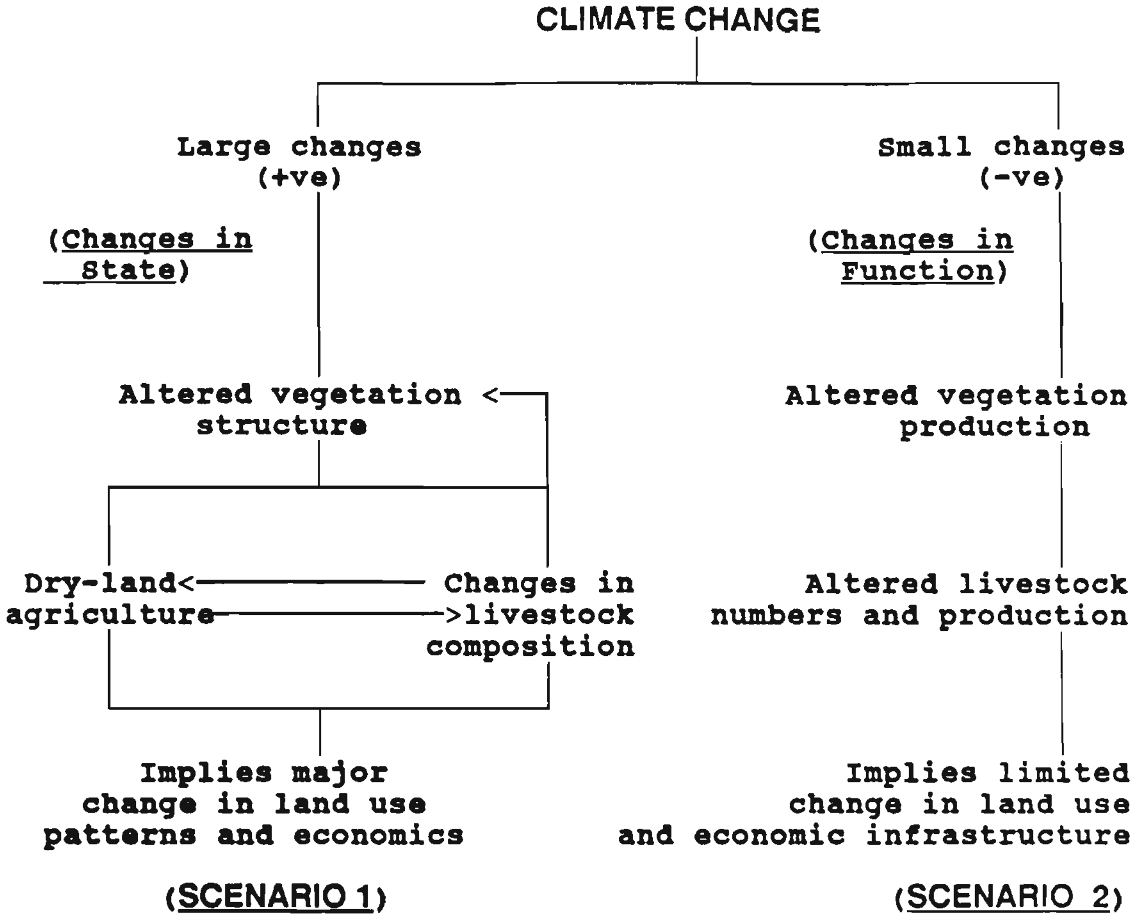


Figure 12. Potential effects of climate change on secondary production and land use in savannas.

Such changes would alter levels of production (Scenario 2, Fig. 12) as well as change the state of the vegetation and the composition of the herbivore communities (including livestock) at the boundaries of savanna lands where they interface with woodlands, grasslands, semi-deserts, and forests. In essence, the boundaries of savannas will shift, while within these boundaries production levels will change.

Alterations in rainfall periodicity (without any change in the mean) may have proportionately larger effects. Large changes in seasonality of rainfall within years, or in variability between years, will alter plant growing seasons, forage nutrient contents, and the ability of herbivores to track forage availability and quality. This may cause a change in state (Scenario 1, Fig. 12).

6.2. Interactive Effects of Climate Change and Grazing. It seems likely that the interactive effects of climate change and herbivores may cause savanna systems to reach the threshold of state changes (Scenario 1, Fig. 12) more rapidly than would climate change alone. This is implied by the feedback (---->) in Scenario 1. Similar situations have been suggested for the long-term change in desert grassland to shrub-savanna in Texas, Arizona and New Mexico. There the combined effects of changes in the seasonality of rainfall (coincident with the termination of the "Little Ice Age") and heavy grazing by cattle may have caused the observed shift in vegetation state (Neilson, 1986).

Another possibility exists, however: browsed woody plants, with minimal woody tissue, appear to be more resistant to drought than unbrowsed plants with a lot of woody tissue to support (Ellis, pers. obs.). In this case, browsing would make the system less susceptible to climate change.

6.3. Effects of Climate Change on Land Use. Changes in the state of savanna systems, caused either by changes in climate variability in the core savannas, or by shifts in average rainfall near the boundaries, are likely to induce changes in the patterns of land use. For example, a change in the ratio of woody to herbaceous plants may force a corresponding change in the ratio of browsers to grazers among livestock herds. Browsers such as goats or camels require different herding strategies and use landscapes differently from grazers such as cattle.

Agriculture can be expected to advance or retreat across the border of wet or mesic savannas, depending on the direction of climate change. Because of the link between ethnographic origins and pastoralism or agriculture, changes in the form of land use (e.g.,. an increase in opportunities for livestock rearing coinciding with a decrease in agricultural potential) implies the possibility of ethnic invasions across previously environmentally (and politically) determined boundaries. Such movements could result in ethnic confrontations.

6.4. Effects of Climate Change on Micro-economic factors. Changes in pastoral practices, for example, away from goats, towards cattle, would require changes in markets and marketing, transportation, and other infrastructural needs. Likewise, a change from a largely agricultural based economy to one dominated by pastoralism would also require major shifts in micro-economic structure and practice.

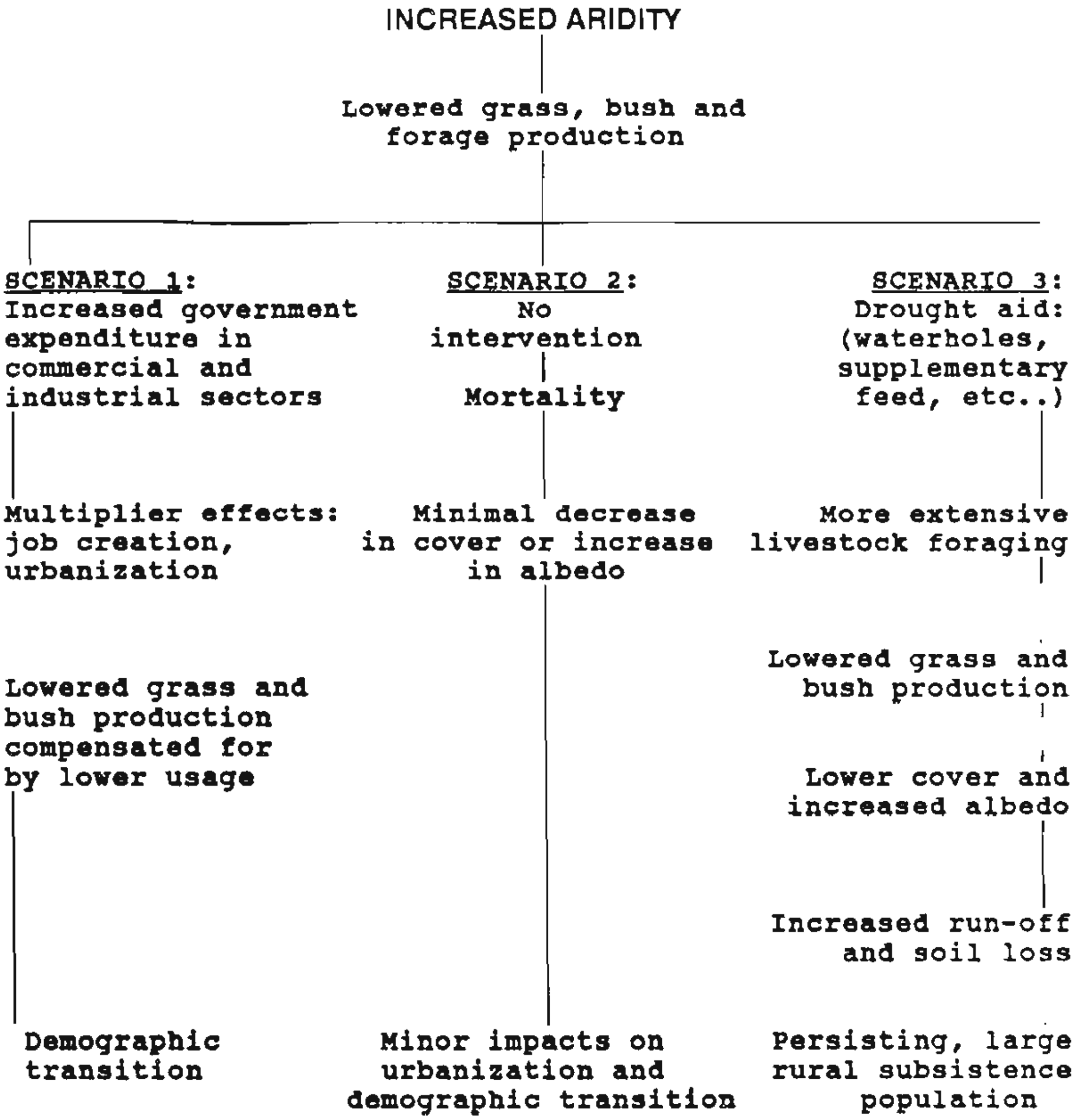


Figure 13. The possible impacts of increased aridity on rural human populations depending on the type of government intervention.

1. The effects of global climate change on savanna structure, composition and functioning in the absence, or in the presence of different kinds, of government intervention in the economies of rural communities.
2. The influence of a global economic recession on land use practices in savannas and the rate of depletion of natural resources.
3. The possible consequences of aid to rural people under contrasting changes in average rainfall.

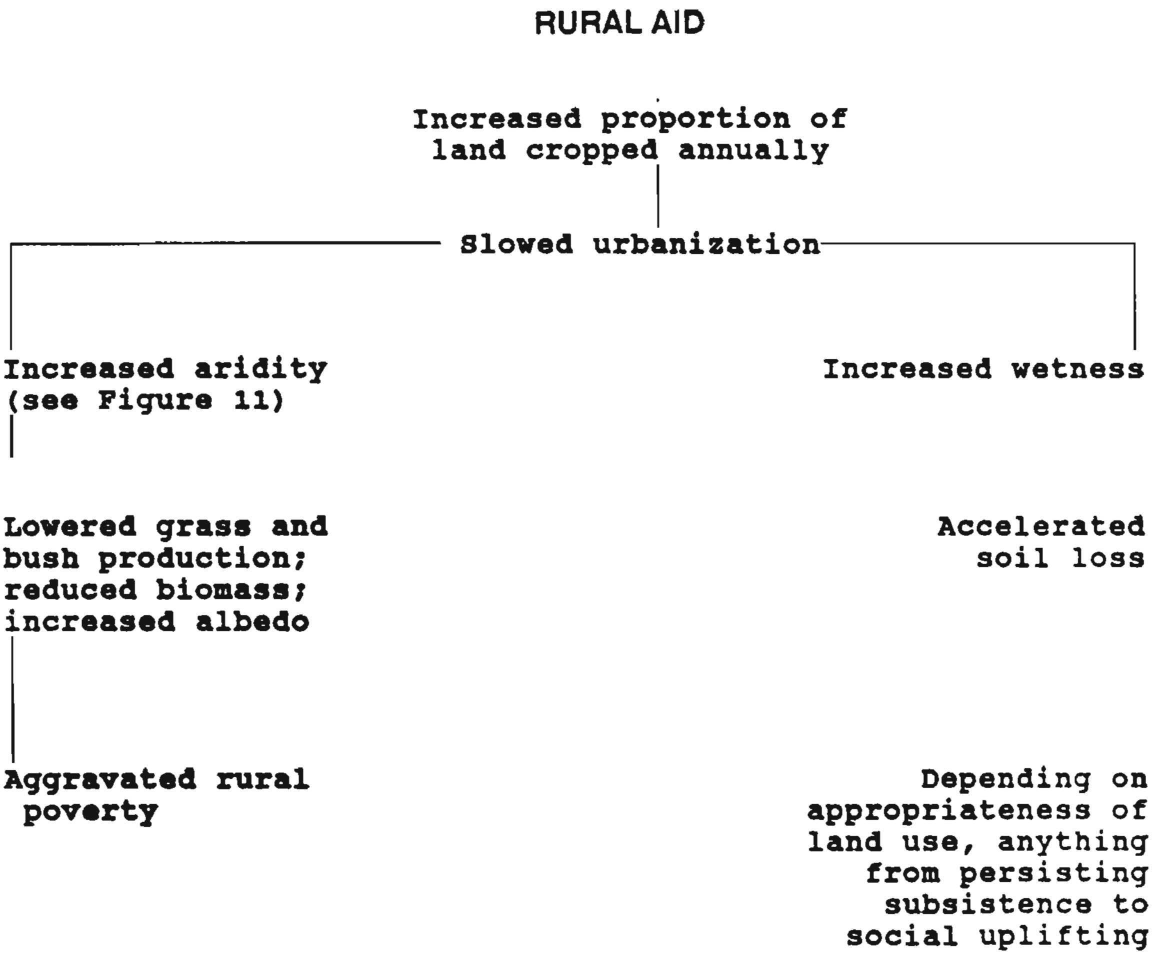


Figure 15. Possible consequences of rural aid as affected by climate change.

Some examples of these possible broader scenarios are shown in Figs. 13 to 15. These are worst case scenarios. Not everything will turn out to be a disaster, and governments and populations can, and hopefully will, take measures to avoid the worst consequences of climatic change. The detailed sequences within each scenario will almost certainly vary with the position of the area in the PAM-PAN plane, and with regional socioeconomic circumstances. Given these conditions, the consequences of the bioeconomic scenarios will probably best be modelled by using current wisdom. The issues are not trivial; although the socioeconomic interventions appear superficially plausible and benign, they have the potential to aggravate conditions regionally, if not globally.

REFERENCES

Abbadie, L., and M. Lepage. 1989. The role of subterranean fungus-comb chambers (Isoptera, Macrotermitinae) in soil nitrogen cycling in a preforest savanna (Cote-d'Ivoire). Soil Biol. Biochem. 21: 1067-1071.

Aucamp, A. J., J. E. Dankwerts, W. R. Teague and J. J. Venter. 1983. The role of Acacia karoo in the false thornveld of the Eastern Cape. Jour. Grassland Society of southern Africa 8: 151-154.

Allen, T. F. H. and T. B. Starr. 1982. Hierarchy. Chicago: University of Chicago Press.

Archer, S. 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. Journal of Biogeography 17: 453-462.

Barbault, P. Lavelle, and M. Lepage. 1985. African savannas. Biological systems of humification and mineralization. In J. Tothill and J. J. Mott (eds.), "Ecology and Management of the World's Savannas," pp. 14-33. Canberra: Australian Academy of Sciences.

Beale, I. F. 1973. Tree density effects on yields of herbage and tree components in South-west Queensland mulga (Acacia aneura F. Muell.) scrub. Tropical Grasslands 7: 135-142.

Beard, J. S. 1953. The savanna vegetation of northern tropical America. Ecol. Mongr. 23: 149-215.

Belsky, A. J. 1990. Tree/grass ratios in East African savannas: a comparison of existing models. Journal of Biogeography 17: 483-489.

Blackmore, A. C., M. T. Mentis, and R. J. Scholes. 1990. The origin and extent of nutrient-enriched patches within a nutrient-poor savanna. Journal of Biogeography 17: 463-470.

Bourliere, F. (ed.). 1983. Tropical Savannas. Amsterdam: Elsevier.

Bourliere, F. and M. Hadley. 1970. The ecology of tropical savannas. Annual Reviews of Ecology and Systematics 1: 125-152.

Braithwaite, R.W. 1984. Problems of scale, complexity and patchiness for sampling vertebrate fauna. In: K. Myers, C. Margules and I. Musto, (eds.), "Proceedings of Workshop on Survey Methods for Nature Conservation" CSIRO, Canberra.

Donaldson, C. H. and D. M. Kelk. 1970. An investigation of the veld problems of the Molopo area. 1. Early findings. Proc. Grassland Soc. of South Africa 5: 50-57.

Frost, P., E. Medina, J. C. Menaut, O. Solbrig, M. Swift and B. Walker. 1986. Responses of Savannas to Stress and Disturbance. Biology International, Special Issue No. 10. 82 pp.

Goldstein, G. and G. Sarmiento. 1987. Water relations of trees and grasses and their consequences for the structure of savanna vegetation. In B. H. Walker (ed.) "Determinants of Tropical Savannas," pp. 13-38. Paris: IUBS Monograph No. 3.

Hills, T. L. 1965. Savannas: a review of a major research problem in tropical geography. Can. Geogr., 9: 220-232.

Hills, T. L. and R. E. Randall (eds.). 1968. The ecology of the forest/savanna boundary: Proceedings of the IGU humid tropics symposium, Venezuela, 1964. Montreal, Canada: Department of Geography, McGill University.

Huntley, B. J. and B. H. Walker (eds.). 1982. Ecology of Tropical Savannas. Berlin: Springer-Verlag.

Knoop, W. T. and B. H. Walker. 1985. Interactions of woody and herbaceous vegetation in a Southern African Savanna. Jour. Ecology 73: 235-253.

McNaughton, J. J. 1985. Ecology of a grazing ecosystem: the Serengeti. Ecol. Monogr. 55: 259-294.

Medina, E. 1987. Nutrients. Requirements, conservation and cycles of nutrients in the herbaceous layer. In B. H. Walker (ed.) "Determinants of Tropical Savannas," pp. 39-65. Paris: IUBS Monograph No. 3.

Menaut, J. C., J. Gignoux, C. Prado and J. Clobert. 1990. Modelling tree community dynamics in a humid savanna of Cote d'Ivoire: effect of fire and competition with grass and neighbours. J. Biogeogr. 17:

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A Hierarchical Concept of Ecosystems. Princeton, N. J.: Princeton University Press.

Parton, W.J., Schimel, D.C., Cole, C.V. and Ojima, D.S. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal, 51, 1173-1179.

Parton, W.J., Stewart, J.W.B. and Cole, C.V. 1988. Dynamics of C, N, P and S in grassland soils: a model. Biogeochemistry, 5, 109-131.

Pickup, G. 1985. The erosion cell - a geomorphologic approach to landscape classification in range assessment. Australian Rangeland Journal 7: 114-121.

Pickup, G. 1991. Event frequency and landscape stability on the floodplain systems of arid central Australia. Quaternary Science Review (in press)

Sarmiento, G. 1984. The ecology of Neotropical Savannas. Cambridge, Mass.: Harvard University Press.

Sarmiento, G. (ed.). 1990. Las Sabanas Americanas. Aspecto de su Biogeografia, Ecologia y Utilizacion. Merida, Venezuela: CIELAT.

Scholes, R.J. 1987. PhD Thesis, University of the Wit-watersrand, Johannesburg.

Sinclair, A. and J. Norton-Griffiths (eds.). 1980. Serengeti: dynamics of an ecosystem. Chicago: Univer-sity of Chicago Press.

Solbrig, O. T. and F. Golley. 1983. A Decade of the tropics. Biology International, Special Issue No. 2.

Solbrig, O. T. 1990. Ecosystems and Global Environmental Change. In R. Corell (ed.) "The Science of Global Environmental Change," Proceedings of NATO Symposium on Global Change. Dordrecht: Kluver Academic Publishers. (in press).

Smith, T. M. and B. H. Walker 1983. The role of competition in the spacing of savanna trees. Proc. Grassland Soc. of South Africa 18: 159-164.

Stott, P. 1984. The savanna forests of mainland South East Asia: an ecological survey. Progress in Physical Geography 8: 315-335.

Stott, P. 1988. The forest as Phoenix: Towards a biogeography of fire in mainland South East Asia. Geographical Journal 154: 337-350.

Tansley, A. G. 1935. The use and abuse of vegetation concepts and terms. Ecology 16: 284-307.

Tongway, D. J. and J. A. Ludwig. 1990. Vegetation and soil patterning in the semi-arid mulga lands of eastern Australia. Australian Journal of Ecology 15: 23-24.

Tothill, J. C. and J. J. Mott. 1985. Management of the World's Savannas. Canberra, Australia: Australian Academy of Sciences.

UNESCO. 1979. Tropical Grazing Land Ecosystems: A State of Knowledge Report. Paris: UNESCO.

Walker, B. H. (ed.). 1977. Determinants of Tropical Savannas. Paris: IUBS Monograph No. 3.

Walker, B. H. (ed.). 1979. Management of Semi-Arid Ecosystems. Amsterdam: Elsevier.

Walker, B. H. 1981. Is succession a viable concept in African savanna ecosystems? In A. West, H. H. Shugart and D. Botkin (eds.), "Forest succession," pp. 431-447. New York: Springer.

Walker, B. H. and J. C. Menaut. 1987. Research Procedure and Experimental Design for Savanna Ecology and Management. Paris: RSSD Publication No. 1

Walker, B. H. and I. Noy-Meir. 1982. Aspects of the stability and resilience of savanna ecosystems. In B. J. Huntley and B. H. Walker (eds.), "Ecology of Tropical Savannas," pp. 556-590. Berlin: Springer-Verlag.

Walker, J. R. M. Moore and J. A. Robertson. 1972. Herbage response to tree and shrub thinning in Eucalyptus populnea shrub woodlands. Australian Journal of Agricultural Research 23: 405-410.

List of Participants

Dr. S. ARCHER
Range Science Dept.
Texas A &M University
College Station
TX 77843-2126
U.S.A.

Dr. R. BRAITHWAITE
Tropical Ecosystems Research Center
CSIRO, PMB 44,
Winnillie, NT 5789
Australia

Professor Braulio Ferreira de Sousa DIAS
Dpto. Regional Geociencias-DF
IBGE - C.P. 04-0270
Brasilia DF - 70.3000
Brazil

Dr. J. ELLIS
Natural Resources
Ecology Laboratory
Colorado State University
Fort Collins, Colorado 80523
U.S.A.

Dr. Peter FROST
Dept. of Biological Sciences
University of Zimbabwe , P.O. Box MP 167
Mount Pleasant , Harare, Zimbabwe

Dr. Malcolm HADLEY
MAB/UNESCO
7, place de Fontenoy
75700 Paris, France

Professor J. J. McCARTHY
Director, Museum of Comparative Zoology
Harvard University
Cambridge, MA 02138
U.S.A.

Dr. Jean-Claude MENAUT
Ecole Normale Superieure
Laboratoire de Zoologie
46, rue d'Ulm
75230 Cedex 05 Paris, France

Dr. M.T. MENTIS
Department of Botany
University of the Witwatersrand
1 Jan Smuts Avenue
Johannesburg 2001, Republic of South Africa

Dr. Ian NOBLE
Dept of Environmental Biology
Research School of Biological Sciences
ANU, GPO Box 475
Canberra, ACT, Australia

Dr. William PARTON
Natural Resources
Ecology Laboratory
Colorado State University
Fort Collins, Colorado 80523, U.S.A.

Dr. R.J. SCHOLES
Dept. of Botany
University of Witwatersrand
P.O.Box 1176
Johannesburg 2000, Republic of South Africa

Professor H.H. SHUGART
Dept. of Environmental Sciences
Clark Hall
University of Virginia
Charlottesville, VA 22903, U.S.A.

Dr. Juan SILVA
Postgrado Ecologia Tropical
Facultad de Ciencias , University of Los Andes
Merida, Venezuela

Professor Otto SOLBRIG
Harvard University Herbaria
22 Divinity Avenue
Cambridge MA 02138, U.S.A.

Dr. Philip STOTT
Department of Geology
School of Oriental and African Studies
University of London
Malet State
London WC1E 7HP, U.K.

Professor Brian H. WALKER
Chief, Division of Wildlife and
Rangeland Research
CSIRO, P.O.Box 84
Lynehrm ACT 2602, Australia

Dr. Patricia WERNER
Director, Biotic Systems & Resources
Room 1140
National Science Foundation
1800 "C" Street N.W.
Washington, D.C. U.S.A.

Dr. David WIGSTON
Dean, College of Natural Resources
Northern Territory University
Box 40146
Casuarina, N.T. 0811, Australia

Biology International
is the News Magazine of the

INTERNATIONAL UNION of BIOLOGICAL SCIENCES

President: J. SALANKI (Hungary)
Vice-Presidents: F. di CASTRI (France)
W.D.L. RIDE (Australia)

Past-President: O.T. SOLBRIG (U.S.A.)
Secretary General: G. NICOLIS (Belgium)
Treasurer: D.F. ROBERTS (U.K.)

Executive Secretary: T. YOUNES

IUBS SECRETARIAT
51, Boulevard de Montmorency, 75016 Paris, France.
Tel: 33 (1) 45.25.00.09 - Telex: c/o ICSU 630 553 F
Telefax: 33 (1) 42.88.94.31

The International Union of Biological Sciences is a non-governmental, non-profit organization, established in 1919. Its objectives are to promote the study of biological sciences, to initiate, facilitate, and coordinate research and other scientific activities that require international cooperation, to ensure the discussion and dissemination of the results of cooperative research, to promote the organization of international conferences and to assist in the publication of their reports.

The membership of the IUBS presently consists of 41 Ordinary Members, adhering through Academies of Science, National Research Councils, national science associations or similar organizations, and of 72 Scientific Members, all of which are international scientific associations, societies or commissions in the various biological disciplines.

National Adhering Organizations

ARGENTINA- Consejo Nacional de Investigaciones Cientificas y Technicas
AUSTRALIA- Australian Academy of Science
AUSTRIA- Osterreichische Akademie der Wissenschaften.
BELGIUM- Académie Royale de Belgique
BRAZIL- Conselho Nacional de Pesquisas
BULGARIA- Bulgarian Academy of Sciences
CANADA- National Research Council
CHILE- Sociedad de Biologia de Chile
CHINA- Association for Science and Technology, Beijing
CHINA- Academia Sinica, Taipei
CUBA- Academia de Ciencias
CZECHOSLOVAKIA- Czechoslovak Academy of Sciences
DENMARK- Det Kongelige Dansk Videnskabernes Selskab
EGYPT- Academy of Scientific Research and Technology
FINLAND- Societas Scientarum Fennica
FRANCE- Académie des Sciences
GERMANY F.R - Deutsche Forschungsgemeineschaft
HUNGARY- Academy of Sciences
INDIA- Indian National Science Academy
IRAQ- Scientific Research Council
IRELAND- Royal Irish Academy
ISRAEL-Academy of Sciences and Humanities
ITALY- Consiglio Nazionale delle Ricerche
JAPAN- Science Council of Japan
JORDAN-Yarmuk University, Irbid, Jordan
MONACO- Centre Scientifique de Monaco
NETHERLANDS- Koninklijke Nederlandse Akademie van Wetenschappen
NEW ZEALAND- The Royal Society of New Zealand
NORWAY- Det Norske Videnskaps Academi
PHILIPPINES- Natioanl Research Council of the Philippines
POLAND- Academy of Sciences

SAUDI ARABIA- King Abdul Aziz City for Science & Technology
SOUTH AFRICA- Council for Scientific & Industrial Research
SPAIN- Consejo Superior de Investigaciones Cientificas
SWEDEN- Kunglige Vetenskapsakademien
SWITZERLAND- Swiss Academy of Sciences
UNITED KINGDOM- The Royal Society
U.S.A.- National Academy of Sciences- National Research Council
U.S.S.R.- Academy of Sciences
VENEZUELA- Consejo Nacional de Investigaciones Cientificas y Tecnicas
YUGOSLAVIA- Union of Biological Sciences