

Section A: Project Summary

Biocomplexity in African savannas

Niall P. Hanan, Robert J. Scholes, Michael B. Coughenour, Luanne Otter,
Philip Omi, Gerhard Dangelmayr

African savannas can be abstracted to a few-component system: trees, grasses, grazers, browsers and fires; whose interaction is mediated by climate, soil and human use. Observational evidence suggests that savanna systems show two primary bifurcations: a long-term one leading to "nutrient poor" savannas or "nutrient rich" savannas, and a relatively rapid one leading to sparsely-treed savannas or densely-treed savannas. Although transitions occur, the potential range of savanna structure and function within the multi-dimensional environmental space is generally not realized because stable states are favored by a combination of interactions and feed-back mechanisms. In our conceptual and numerical scheme, the nitrogen and phosphorus cycles are closely coupled and determine vegetation type; the interaction of nitrogen and carbon biogeochemistry, herbivory and fire then determines vegetation structure.

The three broad objectives of this proposal are:

- 1) To develop a conceptual and model-based understanding of savanna ecosystems that will allow us to predict, with quantified uncertainty, the emergent properties of savannas that result from complex interaction and feedback between climate, soil, herbivory and fire. This will include the change in stable states under varying conditions, the resilience of the different forms to change, and the thresholds between stable states.
- 2) To develop our understanding of the complexity of biological systems from an analytical/systems perspective, using savannas as model ecosystems.
- 3) To enhance future understanding of complex biological systems through graduate and undergraduate training that profits from the research undertaken in this project. To promote graduate and undergraduate teaching of *biocomplexity* and a broader public awareness of the complexity and inter-relatedness of environmental systems.

This proposal brings together an interdisciplinary team with complementary expertise, including savanna ecologists with interests in the carbon and water cycle, nitrogen biogeochemistry and fire ecology, and process based ecosystem modelers teamed with a mathematician specializing in the study of dynamic systems from an analytical perspective. The project will test emerging theory regarding savanna systems with data from long-term manipulative and 'natural experiments'. The synthesis of existing information, for instance on fire exclusion experiments in Africa, is the first step. New data collection will take place on existing long-term experiments, and 'natural experiments' such as nutrient-enhanced patches resulting from human settlement centuries ago. A range of modeling approaches will be used, from analytical to highly detailed dynamic ecosystem models, applied at a range of spatial and temporal scales, from the patch/hour to the continent/millennium.

Section B: Table of Contents

1. Complex interactions in savanna ecosystems
2. Research objectives
3. Methodology
4. Educational Activities
5. Results from Prior Research
6. Project management

Section C: Project Description

1. Complex interactions in savanna ecosystems

Complex systems are characterized by one or more of the following features:

- a medium number of distinctly different components, with high connectivity (systems with a *large* number of *similar* components can be summarized using relatively simple statistical laws, and *small* number systems can be solved deterministically)
- interaction and feed-backs between system properties
- non-linearity of interaction
- time-delay in response

Virtually all biological systems have these attributes to some degree. However, to make progress in understanding complex ecological phenomena, our strategy is to study a system which demonstrates phenomena resulting from complexity, but which is not so complex or poorly understood as to be intractable. African savannas offer such a system.

Savannas are here defined as ecosystems in which the net primary production is shared, to a meaningful degree, by woody plants and grasses. They are thus, at minimum, two-component systems. Of course, typical savanna communities contain many different species of woody plant (henceforth referred to as ‘trees’, although they may include woody shrubs and suffrutices) and many species of grasses and forbs. Trees and herbaceous species have dramatically different properties (Table 1), and their coexistence in savannas remains a problem with many proposed solutions but no definitive answers.

Attribute	Trees	Grasses
Individual Mass at maturity	Large (typically >10 kg)	Small (< 1 kg)
Height at maturity	5-15 m	0.5-2.0 m
Area at maturity	>10 m ²	<1 m ²
Longevity	100 years	1-2 year (in perennial grasses, 6 months in annual grasses)
Sexual reproduction	Relatively few, large seeds, dispersed by dehiscence or animals	Very many, tiny seeds, dispersed by wind or clinging to animals
Vegetative reproduction	Epicormic or root budding following damage is common	Tillering is the dominant method of space occupation
Position of buds	Tips of branches	Base of crown
Interseasonal carbohydrate storage	Enough to support full initial leaf expansion	Only sufficient to create a small leaf area
Leaf nitrogen content	Up to several percent, sustained	Can be initially high, but rapidly declines to below 1%

Table 1. Some attributes of the plant components of savanna systems

Ecologists from Southern, East and West Africa often diverge in their understanding of savanna processes and the relative importance attributed to different driving variables. This is in part because the suite of climatic, edaphic and biotic factors varies widely between these regions. For example, in the savanna grasslands of West Africa the density of wild ungulates is generally too low to impact tree recruitment. The role of domestic animals, the inverse relationship between soil nutrients and rainfall/production and the division between low productivity-high palatability-low fire regions to the north and high productivity-low palatability-high fire regions to the south is invoked to explain patterns in vegetation type, structure and transhumance (Valenza, 1981; Menaut and Cesar, 1982;

Breman and De Wit, 1983; Le Hou  rou, 1989; Hanan et al., 1991). In East Africa the role of wild ungulates and their migratory patterns are considered crucial elements of savanna form, function and heterogeneity (McNaughton, 1983; 1988; McNaughton and Banyikwa, 1995). However, soil chemical and physical limitations on tree establishment is often responsible for the low tree cover, so somewhat less emphasis has been placed on herbivore-tree interactions (Belsky, 1985; 1992; Sinclair, 1995), with some notable exceptions, including elephant effects on tree cover in Masai-Mara (Dublin, 1995). Research in East Africa has also highlighted the interaction of soil chemistry (availability of micronutrients such as Na, K, Ca, etc.) and herbivore behavior (McNaughton, 1988; 1990). Southern African research has emphasized fire, and the interaction of the carbon and nitrogen cycles (Scholes and Walker 1993). An important early activity in this research will be a synthesis of results from the three main regions, and a meta-analysis of the available data, designed to identify common features (or outliers) that will assist in the refinement of the conceptual and analytical models we describe below.

While perceptions differ, our working hypothesis in this proposal is that those perceptions are not mutually exclusive and that they in fact form end-points in the gradients of climate, soil, fire and herbivory across Africa. The 'classical model' of savanna structure and function proposes an equilibrium between woody and herbaceous species mediated by differential access to soil water (e.g. Walter, 1971; Walker et al., 1981). We propose a disequilibrium model in which the linkages between the carbon, nitrogen and phosphorus cycles (all of which are impacted by water and soil) determine the frequency and intensity of grazing, browsing and fire, which in turn determines tree cover. In this model, savanna ecosystems are more complex than in the classical model, including also soil type and nutrient status, herbivory, fire and humans as essential internal components, and the climate as the main external driver. In addition, our conceptual model of savanna systems subdivides the trees into several classes, based primarily on their nutrient physiology (but with many correlates), and adds a nitrogen-fixing component (typically a forb). Herbivory is by mammals or by insects, which are either grazers (grass eaters) or browsers (tree eaters).

1.1. Continental-to-landscape scale patterns: fertile and infertile savannas

The regional to continental distribution of savanna types in southern Africa can be classified in terms of soil type and nutrient status. As a general rule, soils derived from the old and highly weathered African Shield parent materials have few available nutrients, low soil organic matter (SOM) binding capacity and low phosphorus availability. By contrast soils on younger, sometimes volcanic, surfaces to the south of the region, along the Rift Valley, and in the lower rainfall zones to the north and east of the region, tend to be less weathered, with higher available nutrients and higher SOM-binding capacity. The typical soil types of the African and post-African erosion surfaces give rise to the "fertile" and "infertile" savannas (Figure 1).

The fertile and infertile savannas contain distinct assemblages of tree species with contrasting physiognomy. The infertile savannas are typically dominated by trees with relatively large leaves, low leaf nitrogen content (high C:N ratio) and high tannin content. The fertile savannas are dominated by fine-leaf species (mostly bipinnate species in the family *Mimosaceae*), spinescence, and relatively high leaf nitrogen (low C:N). The difference in C:N ratio means that the infertile savannas sustain relatively low mammalian and insect herbivore populations compared to the fertile savannas (Scholes and Archer, 1997). At the continental scale this pattern has apparently been stable for millenia, with adaptation of tree species to particular soil types and coevolution of herbivores. However, it is possible to transform a broadleaf savanna into a stable fineleaf savanna by addition of nutrients (Blackmore et al., 1990), and the reverse transformation may be possible (although more difficult to achieve experimentally).

At regional and landscape scales the fertile/infertile division of soils and associated tree species is

also apparent, driven by geomorphology and soil differences related to catenal position, slope or differential erosion that result in local nutrient depletion or enrichment. Thus the soils and associated savanna vegetation on the tops of the catena in many regions are nutrient depleted relative to the lower slopes, where influx of organic material, silt and clay from upslope locations increases the overall nutrient status (Scholes et al., 2001).

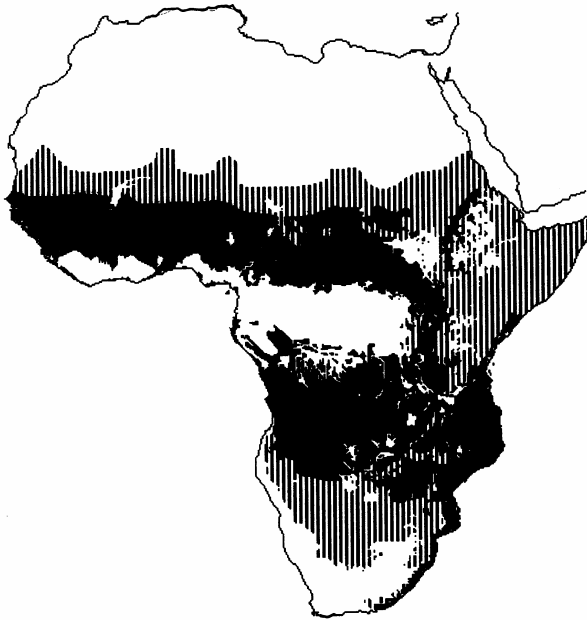


Figure 1. The distribution of fertile and infertile savannas in Africa. Dark-shaded areas are broad-leaf, nutrient-poor, savannas; striped areas are fine-leaf, nutrient-rich savannas. This map was derived from White (1983) by reclassifying woodland and wooded grassland map units into one or other of the two savanna classes according to dominant tree species.

1.2. Continental-to-landscape scale patterns: vegetation structure

Savanna systems can exhibit several alternate states. Firstly, the tree-grass system is apparently unstable in the general case, and in the absence of disturbance (fire, browsing and grazing) savanna vegetation typically converges on a closed woodland endpoint, where further tree growth is limited by tree-on-tree competition, and grasses are reduced to a minor component (Scholes and Archer, 1999). However, in the presence of frequent fires or browsing/grazing, and especially when fires and browsing are combined (Dublin, 1995, Edroma, 1984; Skarpe, 1990), savanna vegetation structure converges on a grassy state with few, scattered large trees (and typically many suppressed trees within the grass layer).

To explain the persistence of open savanna vegetation in Africa we propose a conceptual model that builds on the initial distinction between the fertile and infertile savannas at continental-to-landscape scale and adds disturbance factors that suppress tree cover (Figure 2). In this scheme, savanna structure is controlled by disturbance (rather than competitive equilibrium) but the relative importance of fire, grazing and browsing in suppression of tree cover depends on soil nutrient status and primary productivity. Furthermore, we hypothesize that the stability of the fertile and infertile forms is related to positive feedback mechanisms that promote conservation and loss of N in the fertile and infertile savannas, respectively.

In Figure 2, parent material and weathering history of soils affect phosphorus availability (P), which limits the occurrence and relative importance of biological nitrogen fixation (BNF) by ecto- and endo-mycorrhizal associations. Soil nitrogen availability (N) affects the species composition of trees and grasses and the carbon-nitrogen ratio (C:N) of leaf material. The C:N of plant material affects

palatability and digestibility to herbivores, and thus limits the population density of grazers (G) and browsers (B). Grazing intensity, in combination with seasonal and interannual variations in net production of grasses (NPP), determines available fuel load during the dry season (L) and thus the frequency and intensity of fires (F). Grazers, browsers and fires combine to determine vegetation structure by suppressing (or not) the survival of tree seedling and recruitment of seedlings into the woody canopy layer. Higher grazing and browsing intensity in fertile savannas promotes recycling of nitrogen in urine and feces, conserves N and thus promotes the fertile condition. Low herbivory in the infertile savannas reduces N recycling, increases fuel-load and thus fire frequency and intensity which increases volatilization and loss of N to the atmosphere, reduces buildup of organic matter in the soil, and promotes the infertile condition. Those savannas on the ‘export path’ of the southern African regional circulation are particularly prone to nitrogen loss to the ocean, via the atmosphere.

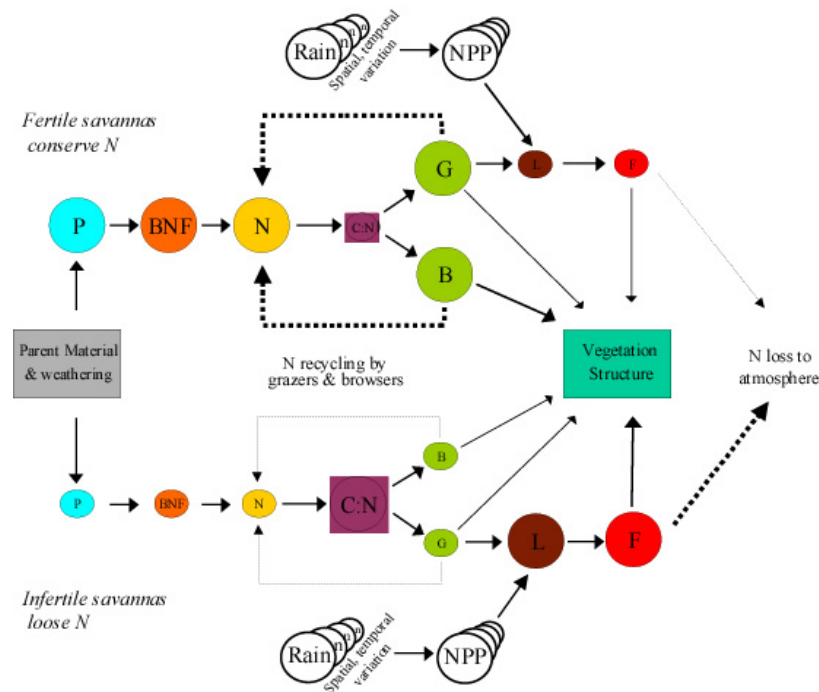


Figure 2. Savanna complexity affecting species composition and structure at continental-to-landscape scales. Box and arrow sizes indicate relative importance of pool or process. Solid arrows indicate primary direction of control and dotted arrows indicate positive feed-back processes that maintain the "fertile" and "infertile" stable states.

Key: P = phosphorus availability, BNF = biological nitrogen fixation, N = soil nitrogen availability, C:N = carbon-nitrogen ratio of leaves, G = grazing intensity, B = browsing intensity, Rain = available soil water on a seasonal-annual basis, NPP = herb layer net primary production, L = standing fuel load, and F = frequency and intensity of fires.

Thus overall, nutrients and water control the system at a lower level, affecting in particular the species composition, productivity and palatability of savannas, but the “structure” (primarily tree cover in this context) is dependant on the complex interactions of herbivory and fire that affect survival of tree seedlings and recruitment into the adult tree population.

1.3. Landscape-to-patch scale patterns: fertile and infertile patches

In addition to regional-scale differences in savanna fertility related to soil parent material, and landscape-scale differences related to geomorphology, fine-scale heterogeneity within savannas, in

particular the presence of localized nutrient-rich patches, is ubiquitous and often considered a central feature of savanna ecosystem function (McNaughton, 1984; Blackmore et al., 1990). These fertile patches are usually the result of very different processes than those described at the broader landscape-to-continent scale. However, we hypothesize that they are similar in respect of the processes that determine vegetation structure and the positive feed-backs that sustain elevated fertility and make the patches relatively stable features of the landscape (Figure 3).

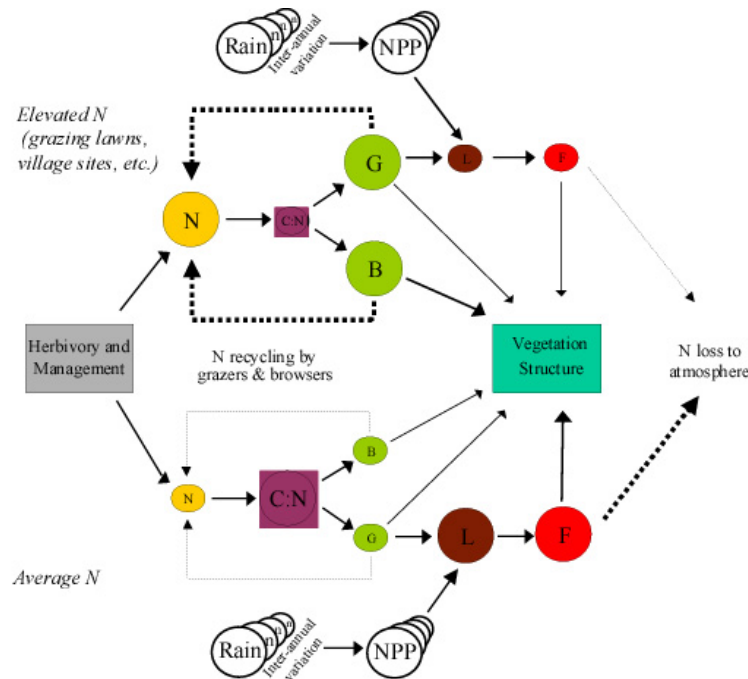


Figure 3. Savanna complexity affecting savanna structure at landscape-to-patch scales. Box and arrow sizes indicate relative importance of pool or process. Solid arrows indicate primary direction of control and dotted arrows indicate positive feed-back processes that maintain the "fertile" and "infertile" stable states. (See Fig. 2 for key).

Figure 3 is similar to Figure 2 except that the differences in nutrient status are related to local processes rather than broad-scale geological or geomorphological factors. Local scale factors that might concentrate nutrients in a particular area include grazing lawns where herbivores preferentially graze or rest, with resulting elevated N-inputs in urine and dung, old village sites, termitaria and canopy-intercanopy differences in the vicinity of larger trees. The initial conditions establishing these patches are hard to predict (e.g. a favored grazing patch may appear following a fire in an area not previously favored). However, once established the processes of nutrient recycling, fire suppression, and the import of nutrients from adjacent areas by herbivores, can result in considerable stability.

1.4. Stable states and transitions in African savannas

The complex of interacting factors that control savanna ecosystem structure and function at patch to continental scales (i.e. Figures 2-3) do not, in practice, result in a multitude of savanna types distributed across the various gradients. Rather, despite the complex environmental and "driver" space (in particular the potential, if not realized, gradients in herbivory and fire frequency), the range of savanna types actually expressed in Africa is relatively condensed (Figure 4).

Figure 4 implies that African savannas exist within a two-dimensional environmental "space". However, both nutrient and recruitment axes are complex variables with many interacting

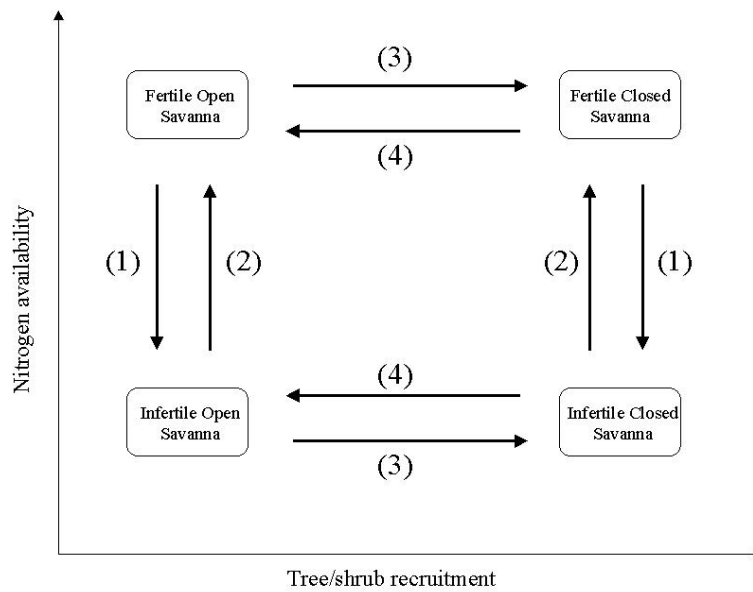


Figure 4. Stable states and transitions in African savannas. Soil N availability is related to parent material and weathering rates that influence biological nitrogen fixation (P-limitation), import and export of N (herbivores, humans, fire). Tree recruitment is related to browsing and grazing intensity, seasonal weather variations and fire frequency/intensity.

Transition	Description	Example scenarios at continental to landscape scales (a) and at landscape to patch scales (b)
1	Fertile to infertile	a) Decline in soil fertility as soil weathers (P declines) during millennial time-scales b) Imposed high fire frequency with low grazing intensity reduces N at decade to century time scales
2	Infertile to fertile	a) Gradual build-up in N status when N inputs (e.g. industrial N deposition) exceed losses in fire and trace gas emissions. b) Nutrient redistribution/concentration in the landscape, e.g. herbivore-favored grazing lawns, old village sites, termitaria, etc.
3	Open to closed	a) and b) Replacement of wild herbivores by high and sustained populations of domestic cattle, especially with concurrent fire suppression
4	Closed to open	a) and b) Severe disturbance of tree population caused by, for example, fire after drought or pest/disease outbreak

Table 2. Transitions between stable states in African savanna. Some transitions may occur under current conditions or can be induced experimentally, others are less easily observable/are hypothetical.

contributing variables as indicated in Figures 2-3. While climate has clear effects on species composition and productivity, the fertile/infertile and open/closed schematic is valid across the range of African savanna climates. Furthermore, the definition of "closed" in this scheme (i.e. the percent canopy cover of trees) is often a function of the nutrient status of the soil and climate controls on net primary productivity. Note also that the closed form we envisage is still "savanna" as defined, although herbaceous production is relatively low. Thus African savannas appear to gravitate to one of four primary "attractors" that are relatively stable and self-maintaining. The reasons for this have already been discussed in part: they include the relatively clear dichotomy in soil nutrients (particularly P) between old and young soils, the feed-backs between herbivory, fire and nutrient status, and the self-sustaining influence of herbivory and fire on savanna structure.

In this section we discuss the ways in which savannas may be induced to transition from one stable state to another, the resilience of the stable states, and the likely thresholds between states (Table 2). We expect that in most situations, "resilience" and "threshold" will be interrelated and dependent on time (i.e. duration of effort). Some transitions are frequently observed or can be easily induced experimentally. Others are rare in practice, may be difficult to induce experimentally, and, because of high effort requirement, may be more hypothetical than actual. **It is the identification and quantification of the transitions, resilience and thresholds in savanna ecosystems that forms the heart of this *Biocomplexity in the Environment* proposal.**

There are numerous examples of savanna community state transitions. For example, the savanna vegetation of the northern Serengeti plains apparently changed from open grassland to closed shrubland around the turn of the 20th century, in large part because *rinderpest* reduced wildebeest and human populations (with decreased fire frequency). However, in the 1950's the woodlands and thickets rapidly declined because of increased browse and fire and returned to the open form now widespread across the Serengeti (Sinclair, 1995). The savannas of South Africa, Namibia and Botswana have, in many documented cases, changed from an open to closed state following the widespread adoption of commercial cattle ranching (eg van Vegten, 1983).

However, many questions and unknowns remain. For example, why have the relatively stable fertile patches within the infertile zone not coalesced during the millennia? We hypothesize that it is in part because the overall N of the landscape is limited, thus the fertile patches are "harvesting" N from surrounding areas and areal coverage is limited by supply. In addition, the rate of formation of fertile patches may be balanced by the rate of loss since, when abandoned by the factors increasing fertility, the fertile patches have little autonomous ability to sustain higher N-status and thus may gradually relax back towards the infertile state.

Similarly, we know that the closed form is the usual end-point in savanna systems where herbivory and fire are suppressed and that, once established, the closed form is rather stable. Why, then, have not small patches of closed savanna persisted and gradually increased in coverage over the millennia (as rare or random events allow the formation of new closed forest patches)? Is it that the factors favoring the open form (fire and herbivory) can still operate even when a system has migrated substantially toward the closed form? For example, 'bush encroached' areas in Namibia are currently undergoing a fungal disease attack which may lead to widespread tree die-back. Thus, at a landscape scale, factors favoring formation of closed savanna are in equilibrium with factors that can transform a closed savanna back to the open form. The research proposed here will allow us to examine these questions and test hypotheses explaining the observed patterns.

2. Research objectives

From past studies in savanna ecology we know many of the aspects of savanna function and dynamics and can paint a conceptual picture of the interacting factors that create particular savanna types and structures, and we can hypothesize the factors that lead to relative stability in these states.

However, we understand little of the complex interactions that operate between stable states, or the location and nature of the thresholds and feedbacks that divide the multi-dimensional system. In this study we seek to explore and, where possible, quantify the complex interactions that result in multiple stable states and which define the intervening environmental "space", and thus the combination of factors, the strength and thresholds of those factors, that can lead to state-transitions.

Our overall objectives are stated below, together with general "systems level" hypotheses. More detailed "process level" hypotheses are given in the methods section.

Objective 1: To develop a conceptual and model-based understanding of savanna ecosystems that will allow us to predict, with quantified uncertainty, the emergent properties of savannas (functional type, structure) that result from complex interaction and feedback between climate, soil biogeochemistry, herbivory and fire.

Accepting that processes in savanna ecosystems can be greatly affected by rare, random or chaotic events as well as quasi-continuous processes, we will develop the simulation model to incorporate statistical approaches where necessary to predict stable states, thresholds and likely trajectories of savanna ecosystems under historical conditions and varying alternative scenarios.

Hypothesis 1: A single minimally-complex model of savanna ecosystem function based on the interaction of biogeochemistry, climate, herbivory and fire can predict distributions of savanna type and structure in Africa consistent with observations at regional to continental scale.

Hypothesis 2: The model will reproduce the state transitions resulting from both random and sustained processes at patch, landscape and regional scales, also consistent with observations.

Objective 2: To develop our understanding of the complexity of biological systems from an analytical/systems perspective, using savannas as model ecosystems.

Use savanna ecosystem models of varying complexity to examine the nature of system behavior with respect to climate, soil biogeochemistry, herbivory and fire through analysis of the combination of factors that can cause state transitions and the non-linear interaction of biotic and abiotic factors.

Hypothesis 3: Savanna ecosystems have several alternate stable states, for which the transition thresholds and resilience can be determined by systems analysis.

Objective 3: To enhance future understanding of complex biological systems through graduate and undergraduate training that profits from the research undertaken in this project. To promote graduate and undergraduate teaching of *biocomplexity* and a broader public awareness of the complexity and inter-relatedness of environmental systems.

This component of the project will include undergraduate curriculum development as well as graduate student and post-doctoral training in the field of biocomplexity. We will use savanna systems as our primary model, drawing also on research in other fields of *biocomplexity*.

Successful achievement of these objectives will contribute to the theoretical understanding of savanna ecosystems in general and African savannas in particular. It will contribute to our understanding of *biocomplexity* in ecosystems, the ways in which complexity can be described and analyzed and the ways in which even complex systems can be predicted and managed.

3. Methodology

3.1 Synthesis Activity

The savanna ecology communities in southern, east and west Africa are historically separate and have evolved differently. The local conditions and primary influences are very different, leading to qualitatively different concepts of savanna processes and controls. However, we feel that the underlying processes are similar and that a reanalysis of historical data and a meta-analysis concentrating on the factors influencing savanna type and structure might lead to convergence. There

is a rich array of experimental data from the three regions which has not been synthesized at a continental level. The activity will involve data collation, meta-analysis and synthesis of results, and will proceed by the holding of three workshops, with data tasks in between. The first workshop will identify data sources suitable for synthesis; the second will involve the collation and review of data, and the third will generate synthesis papers. The workshops will be held in the three different regions of African savannas, both to promote the spread of knowledge, and to expose ecologists familiar with one region to the ecology of other regions.

3.2 Savanna Ecosystem Models

Two classes of model will be used to simulate vegetation dynamics and biogeochemistry at a range of scales. These will include a savanna ecosystem model already developed by the investigators that simulates vegetation processes at patch to regional scales and a new class of continental-scale biogeochemical model, operating over millenia, which will be developed for the project based on data collected during the SAFARI 2000 experiment.

Vegetation dynamics, growth and nutrient cycling, will be simulated using a model developed to represent the complex interactions between savanna trees and herb layer (the SAVANNA Model; Coughenour, 1992; 1993). SAVANNA is a spatially explicit, process-oriented model of grassland and savanna ecosystems. The model simulates processes at landscape to regional scales over annual to decadal time scales at 1-7 day time-step. It is composed of sub-models describing soil hydrology and runoff/run-on, soil nutrient dynamics, plant biomass production, multi-species plant population dynamics and large herbivore dynamics. The model aims to produce realistic representations of ecological change in vegetation communities exposed to different climatic, edaphic and management regimes. The model simulates the interactions between plant populations, between plants and herbivores, and the dynamic effects of disturbance, climate and climate anomalies (e.g. drought).

SAVANNA simulates the landscape at three nested spatial scales. At the coarse scale, the region is represented by grid-cells of variable dimension. Within grid-cells, different vegetation types, geomorphological features or management regimes (including agriculture) occupy different proportions of the area. Within each sub-area, trees, shrubs and herbaceous functional types are simulated dynamically, with the relative cover of each depending on the recruitment of saplings into adult age classes and competitive outcomes. The hierarchy of spatial scales facilitates simulation of fine-scale features in the landscape while retaining a grid-cell dimension suitable for regional analyses. The SAVANNA model has been used successfully in a variety of African savanna systems (Coughenour, 1991; 1992; Coughenour and Chen, 1994). SAVANNA requires information on soils, vegetation type and topography as well as average temperatures, humidity and rainfall to simulate weekly NPP, growth and soil physical and biogeochemical processes.

SAVANNA incorporates the impact of fires and herbivory on vegetation structure and biomass. Trace gas (NO_x) emissions from fires are not yet included but will be added during this research. Burn efficiency and emission factors for CO₂ and NO_x, will be based on relationships derived during SAFARI-92 and other experiments (Hao et al., 1988; Lacaux et al., 1996; Scholes et al., 1996; Shea et al., 1996; Stocks et al., 1996; Ward et al., 1996). Simulations of vegetation growth, senescence and decay, and water content across the landscape will provide the information on fuel load, fuel type and fuel quality essential to estimate fire intensity and effects. Estimates of biogenic emissions of NO_x will be based on earlier research in African savannas and elsewhere (Otter et al., 1999; Parton et al., 2001).

A 'millenium' model will be developed specifically for this project. It will be a radically-simplified 4-patch savanna ecosystem biogeochemistry model. The 4 patches will be 1) P and clay-rich substrate on continental deposition path 2) the same on export path 3) P and clay-poor substrate on continental deposition path 4) the same on the export path. 'Lumped parameter' models of the linked C, N and P

cycles, (based on CENTURY model runs), using emission, deposition and transport data from SAFARI 2000, will be run on an annual time-step for approximately 100,000 years. These model simulations will test the hypotheses that the nitrogen status of African savannas is ultimately a function of the balance between N fixation, N deposition and N losses due to fire and denitrification, and that the outcome is dependent on phosphorus availability and geographical location in relation to the continental-scale circulation.

3.3 Uncertainty assessment

Our approach to uncertainty estimation with both ecosystem models will use a Monte Carlo approach as follows: base-line simulations will in all cases use our best estimates of parameter values to determine central tendencies. The uncertainty range will then be determined using a Monte Carlo randomization in which the model is run with a large number of independent parameter sets. In each parameter set, the parameters are randomized within physically/biologically feasible bounds, using a normal distribution weighting around our prior best estimate of the parameter value. This exercise produces a range of predictions from which confidence intervals can be selected using, for example, the 5th and 95th percentiles of the predicted values.

3.4 Patch to landscape-scale data and hypothesis testing

Long-term experimental manipulations: Long-term fire trials exist in many places in Africa. Some have now been discontinued, so an action to capture their information content is urgent. The Kruger Park Fire trials are an example: they have 11 treatments (different frequencies and seasons of fire, including complete exclusion, replicated several times in each of 3 major environmental regions) and have been maintained for over 40 years. Similar experiments exist in Zimbabwe (Matobo Research Station), Zambia (Ndola) and Nigeria. This project will collate and synthesize published (including grey literature) data and results from these experiments. If necessary, supplementary data will be collected from the sites: for instance on soil, climate and plant parameters, allowing the SAVANNA and ‘millenium’ models to be run for each of the treatments at each of the sites and the output compared to observed trends. The objective is to test the hypotheses that

- savannas are intrinsically unstable, and in the absence of fire trend towards closed woodlands at a rate which can be predicted from soil and climate conditions.
- Thresholds of fire intensity and frequency exist which keep the savanna in an open state.

Publication of the results will be in collaboration with site and data custodians.

Grazing intensity trials also exist in several places. An excellent example is at Sandveld in Namibia, where 4 levels of stocking, fully replicated at landscape scale, have been maintained for 20 years. There are similar experiments in South Africa (Towomba, Fort Hare) and elsewhere (see O'Connor, 1985), and a wide range of ‘opportunistic’ experiments resulting from different land use histories (eg Parsons et al., 1997). The project will collate published and ‘grey’ data from a selected set of these experiments, supplemented by new site data where necessary, in order to test the hypotheses that

- increasing grazing intensity reduces fire intensity and thus promotes tree recruitment
- increasing browsing reduces tree recruitment, particularly in the presence of fire.

Long-term fertilization trials on natural vegetation in Africa are extremely rare. There was a set in South Africa in grasslands, which have now been lost – an example of the importance of collating the data while they are still available. The fertility aspects of the study will need to rely on ‘natural and opportunistic’ experiments.

A synthesis of long-term tree-clearing experiments in savannas throughout the world is currently the subject of a National Center for Ecological Analysis and Synthesis (NCEAS) activity, to be completed in 2001. That study, which includes PIs from both NREL and CSIR, has addressed

hypotheses regarding the competitive effect of trees on grass production. The data from that study will become part of a public domain set held at Oak Ridge National Laboratory (ORNL-DAAC).

Opportunistic and natural experiments: Fenceline contrasts between areas exposed to different grazing and fire regimes exist in many parts of Africa. Data on the site characteristics (sufficient to run the models: climate, soil and vegetation), and contrasting management regimes (stocking rates, fire frequencies), will be collected for a limited sample of such contrasts throughout Africa. We will include three 'replicates' in each of the four quadrants of the nutrient x water availability plane (i.e. high and low water and nutrient status for a total of 12 sites, each with two management treatments). These sites will be used to test the hypotheses that

- intensified grazing accompanied by a reduction in fire intensity leads to increase in tree cover (unless balanced by harvesting of wood for human use)
- rate of increase in woody cover is greatest on clayey fertile soils

Similarly, old settlement sites, which show the effects of nutrient enhancement many decades or centuries ago, exist throughout Africa. Nutrient (particularly phosphorus) enriched patches will be sought and sampled on both low-P and high-P soils in southern Africa (eight sites, each with 2 'treatments'), based on archeological records, to test the hypothesis that

- N fixation (as evidenced by the N content of the vegetation, and the presence of known BNF species) is increased in low P savannas when P is added over a long period of time.

Contrasts between clayey (fertile) and sandy (infertile) soils occur in many places, under the same climate. Usually, the difference in the physical properties of the soil, which profoundly affect its water relations, are confounded with the nutrient effects. The gradients in rainfall in southern Africa (Kalahari Transect, Scholes and Parsons, 1997) and West Africa (SALT transect) can be used to explore the effects of climate while controlling for variations in soil, and the effects of soils, while controlling for climate. Satellite remotely sensed data (including public domain AVHRR and tree cover data, and MODIS and IKONOS data from SAFARI 2000), plus already-collected field data for about 30 locations will be used to test the hypotheses that

- The slope of the accumulated NDVI versus rainfall curve (the 'rain use efficiency') is higher on fertile than infertile substrates
- The landscape-scale tree cover occupies an envelope whose upper limit is a highly-predictive function of climate and soil type, and which shows a bifurcation into dense and sparsely-treed savannas above a rainfall of about 500 mm per annum.
- Fire frequencies are a bell-shaped function of rainfall (infrequent in dry areas, rising to a maximum around 1200mm, and declining sharply above that) and are more frequent on infertile than fertile soil types

3.5 Regional to continental-scale data and hypothesis testing

Savanna nutrient status: The distribution of savanna types across the continent depends on soil type, soil history and climate. The "Millenium" model described above will be parameterized using the new IGBP soils database for Africa (IGBP, 1999), long-term average climate and SAFARI-2000 data on nitrogen deposition, fire frequency and trace gas emissions. The simulations will be used to determine the likely trajectories in system nutrient status, and the sensitivity/stability of the fertile and infertile savanna to subtle changes in climate. Furthermore, simulations of system nutrient status over millennial time-scales will allow us to test the hypothesis that, at the continental scale, savanna form and function ultimately depend on phosphorus controls on nitrogen fixation and/or the net flux of nitrogen to or from the system. Net nitrogen flux is, in turn, dependent on the balance of losses to the

regional atmosphere during fire and denitrification versus deposition of nitrogen from upwind locations.

Savanna structure: The variation in savanna structure (i.e. woody cover in this context) across the continent depends on the combination of soil, climate, herbivory and fire regime. We will use the SAVANNA model, parameterized using regional maps of soil, climate, herbivory and fire frequency to predict savanna structure during a period of approximately 150 years (19th and 20th Centuries). These simulations will be used to predict the average woody canopy cover and its spatial and temporal variability under conditions prevailing during that time. The simulations will be carried out using a 20 km grid (with sub-grid simulation of tree and grass interactions) and weekly time-step to predict the competitive balance between trees and grasses and the ways in which that outcome varies with soil, climate, herbivore density and historical fire frequency. These predictions will be compared with actual woody canopy cover estimated using remote sensing data at 1 km resolution (DeFries et al., 1999).

3.6 Complex system analysis

The numerical modeling and data analyses described above will be used to test and falsify hypotheses and to develop our ability to predict savanna ecosystem behavior under varying conditions. To increase our understanding of system behavior, and especially to develop our ability to analyze and describe the complexity of the systems we are studying, we will also carry out model- and data-based systems analysis. Graphical analyses, of the sort pioneered for savannas by Walker et al (Walker et al., 1981; Walker and Noy-Meir, 1982) will be constructed using the more highly-parameterized models to provide biophysically-realistic analytical parameters and functions. These will be used to explore the topology of the parameter-space in which alternate stable states exist, and to predict the location of the thresholds (and their constancy in relation to the rate and direction at which they are approached by the system).

The simplified analyses will be complemented by the abstraction of the ecosystem models as dynamical systems depending on parameters. Discrete dynamical systems (iterated maps) will be derived from our complex model and simplifications at various scales will lead to a hierarchy of maps of different complexities, including approximations through ordinary differential equations on short time scales which are easier to investigate analytically. The dynamical systems models will be studied using the qualitative and quantitative methods of nonlinear dynamics and bifurcation theory. These studies concern in particular the parameter dependence of stable and unstable fixed points, the sizes of the attraction basins of the stable fixed points and the bifurcations that lead to the creation or annihilation of fixed points or to transitions to periodic, quasiperiodic or chaotic attractors. The dynamical systems analysis will be pursued on different levels of complexity with the aim of finding the simplest model able to describe observed phenomena. These analyses will permit the formal analysis of parameter space topology and identification of thresholds under varying scenarios.

The complex system analysis will serve three purposes:

- to provide quantitative, rigorous analyses of concepts such as stability and resilience
- to teach advanced systems analysis
- to communicate the behavior of complex systems to scientists and the general public in a form which is visual and simple enough to grasp

4. Educational Activities

The educational component of this project will take several forms, including undergraduate, graduate and post-doctoral training. We plan to develop a new undergraduate course at CSU on savanna ecosystems that will complement and augment historical strengths in grassland and rangeland

ecosystems in the Department of Rangeland Ecosystem Science. This course would focus on the complex interactions of physical and biological processes in savannas, the interactions of water, nutrients, fire and herbivory, and effects on productivity, structure and stability of vegetation associations and the density and composition of herbivore and carnivore communities. We propose to employ at least two graduate students at CSU who would focus on the interactions of fire and herbivory with vegetation structure and biogeochemistry. We also plan to develop a graduate seminar in “*biocomplexity*” which would take a broad approach to the subject, with input from the investigators, research associate and graduate students. The graduate students would be encouraged to take a lead role in this seminar to improve their familiarity with the different aspects of *biocomplexity*. The seminar would solicit input from a range of funded *Biocomplexity* projects to compare approaches to description and analysis of complex systems at a range of scales (cellular-global) and synthesize early results. The outcome of this seminar would be the development of curriculum materials for a comprehensive graduate-level course in *biocomplexity* that would be offered by the investigators in later years of the project. The post-doctoral research associate would receive additional training where necessary in savanna ecology, complex system modeling and non-linear system dynamics.

The workshops planned in this proposal will bring together some 12-15 leading savanna ecologists who concentrate their research in different regions of Africa. These will include both local scientists and scientists from North America and Europe who have research ties to the continent. The workshops will challenge our preconceptions regarding savanna function in the light of alternative concepts and data from other ecologists and other regions. We will further be challenged to recast our perceptions in terms of the complex interactions and feed-backs that define the ways in which savanna ecosystems respond, and are adapted to, varying biological and physical factors across a range of temporal and spatial scales

5. Results from Prior Research

5.1 Results from Prior NSF Support

Mike Coughenour is PI of the Integrated assessment of African savannas with spatial-dynamic vegetation and land use modeling.” (NSF/MMIA DEB, \$450,000, M. Coughenour, J. Ellis, PIs, 9/97-9/01). This ongoing project aims to improve our understanding of the combined roles of herbivory, fire, soil, and climate, in the vegetation dynamics of East African savannas. The SAVANNA ecosystem model is being parameterized for the Greater Serengeti Ecosystem. Field studies were designed to improve understanding of the current vegetation distributions and responses to climate, soils, fire, and herbivory. Using a multi-scale sampling design, we sampled vegetation composition throughout the Serengeti National Park and the Ngorongoro Conservation Area. The data have been used to create maps of woody canopy cover, size class distribution of woody vegetation, tree density, herbaceous biomass, and herbaceous dominant species. We have conducted a study of the spatial patterning of elephant impacts within the Seronera woodlands and associations with vegetation heterogeneity. Higher levels of browsing impacts were associated with areas of higher vegetation heterogeneity. Analyses are being conducted to identify the spatial scales at which elephant damage is most significant. These results are being used in the SAVANNA model to understand the relative roles of climate change, herbivory, and fire, in determining the structure and function of savanna ecosystems.

5.2 Other Results from Investigator Research in Savanna Ecology

Dr Niall Hanan has been involved in research into savanna form and function in West and Southern Africa since 1986. Research in West Africa included study of the controls on Sahelian rangeland production and livestock impacts, savanna carbon, water and energy balance and measurement of

savanna function using remote sensing techniques (Hanan et al., 1991; 1993; 1995; 1997a; 1997b; 1997c). During this research, Hanan developed savanna-specific numerical models of radiative transfer and carbon exchange suitable for use in climate system and biogeochemical models (Hanan et al., 1998; Hanan, 2001). In Southern Africa, Hanan is PI of the Kruger Park eddy covariance study that is now collecting long-term and near-continuous measurements of CO₂, water and energy exchange that compare land surface-atmosphere exchanges over two regionally important savanna types, a fine-leaf *Acacia* savanna and a broad-leaf *Combretum* savanna (Hanan et al., 2000). The study is investigating the behavior and controls on savanna function, contrasting fine-leaf/broad-leaf and fertile/infertile savanna types under similar climate.

Dr Robert (Bob) Scholes was PI of the South African Savanna Ecosystem Project based at Nylsvley, 1987-1991. This project, which began in 1974 and ended in 1991, was one of the major sources of information regarding savanna ecology in general, and African savannas in particular. The results were synthesized in a book (Scholes and Walker, 1993) which is a standard and widely-cited text on savanna ecology. The fundamental distinction between fertile and infertile savannas (as opposed to the previous distinction between moist and dry savannas) originated from this work. Dr Scholes' PhD work during the early 1980's was on competitive interactions between trees and grass in savannas; it showed that the classical model was an inadequate explanation and began the trend to disequilibrium models of savanna coexistence. He is a coauthor of a major review on the subject (Scholes and Archer, 1997). His current work is in biogeochemistry, particularly in African savannas (Scholes, 1993, Ellery, Scholes and Scholes 1995), and in relation to fire (Scholes et al., 1996). His findings showed that the emissions due to fires were a tenth of previous estimates, and that the aerobic nitrification (NO_x) emissions were much larger than previously thought (Parsons et al., 1996). He is PI of the SAFARI 2000 regional biogeochemical experiment, which is demonstrating the continental redistribution of nitrogen and its export into adjacent oceans; results will be presented this year.

Dr. Mike Coughenour was a lead investigator in the South Turkana Ecosystem Project (NSF BSR-9007303, \$400,000, 7/90-6/92, J. Ellis, P.I., D.M. Swift, M.B. Coughenour, and J.T. McCabe, co-PI's; and other previous NSF grants 1982-1990). This was a study of nomadic pastoralists and their interactions with a dry savanna/woodland ecosystem in Northern Kenya. Vegetation structure in tropical savannas and dry woodlands was shown to be hierarchically constrained by physical factors: by climate at regional scales, by topography and geomorphology at landscape scales and by water redistribution and disturbance at local and patch scales (Coughenour and Ellis, 1993). The role of competition between trees and grass for soil moisture in determining vegetation structure appeared to be secondary. Physical heterogeneity on the Turkana landscapes ultimately resulted in spatial and temporal variation in plant production and phenology, plant life form diversity, and refuge areas for pastoralists. These in turn contributed to persistence by reducing variability of ecosystem energy flow and long-term variations in species diversity. The SAVANNA landscape model of ecosystem function (Coughenour, 1991a; 1991b; 1992; 1993) was developed. The model provided insights about the spatial components of herbivory in ungulate and pastoral ecosystems (Coughenour, 1991c), and suggestions for using GIS, spatial-dynamic modeling, and remote sensing to improve understanding and management of these ecosystems (Coughenour 1991a; 1992).

Mike Coughenour is also PI of the Integrated Modeling and Assessment System for Balancing Food Security, Conservation, and Ecosystem Integrity in East Africa."(Coughenour, PI, USAID. Global Livestock Collaborative Research Support Program, 1996-2000). Spatial components of pastoral ecosystems have been disrupted by competing forms of land use, with negative implications for ecosystem persistence. Pastoral movements have been increasingly restricted by game reserves, agriculture, land subdivision, and privatization. An integrated modeling and assessment system (IMAS) has been developed that integrates computer modeling, geographic information systems,

remote sensing, and field studies to provide information necessary to conserve biodiversity, wildlife, and ecosystem integrity while increasing pastoral food security.

Dr Luanne Otter was involved in research on the long-term fire plots in the Kruger National Parks (Otter, 1992). The project investigated the effect that different fire regimes had on the size of the C and N soil pools. Her interests also include other aspects of savanna biogeochemistry, including research into biogenic emissions of NO_x and methane from soils and plants and VOC emissions from savanna tree species (Otter, 1995; Guenther et al., 1996; Otter et al., 1999; Otter and Scholes, 2000). Results from this research suggest that NO emissions from the fertile and infertile savanna patches were not significantly different and that soil physical properties may have a greater control over emissions than the chemical properties (Scholes et al., 1997; Otter et al., 1999). Dr Otter has also been involved in a number of projects looking at atmospheric aerosols and nitrogen deposition in SA savannas (Puxbaum et al., 2000; Limbeck et al., 2001). Dr Otter continues her work in biogeochemistry in the SAFARI 2000 project, and recently conducted field experiments focused on N cycling, along the Kalahari sands (Feral et al., 2001). Results indicate that NO fluxes decrease with decreasing temperature and moisture. The SAFARI 2000 project is a regional scale project and involves modeling the fluxes from a local to a regional scale. Results from this work will be analyzed and published over the next two years.

6. Project management

Dr. Niall Hanan will oversee the project and coordinate the activities of the investigators, research associate and students. Hanan will take the lead in collation and preparation of data at regional scale for modeling activities and comparison with regional remote sensing data products. Hanan will work with the research associate and students in developing site-based and regional datasets, modeling activity and analysis, and analysis of physical and biophysical measurements from the Kruger Park eddy covariance study. Hanan will also take the lead in developing undergraduate and graduate-level classes and seminar series. Dr. Robert Scholes will coordinate contacts with savanna ecologists in Africa for collation and synthesis of perceptions and site-based measurements. This will include organization of the Savanna Process Workshops planned under this proposal. In several cases data have already been collated (under an NCEAS Tree-Grass activity), and Scholes has been instrumental in collection of data at a range of sites in southern Africa. Scholes will also coordinate between this project and on-going regional research programs (SAFARI-2000, Africarbon) that are measuring and modeling important processes at site and regional scales related to carbon and trace gas dynamics and savanna biogeochemistry. Dr. Michael Coughenour will oversee modeling activities with the Savanna model, site and regional-scale simulations. This will include working with the research associate and graduate students to enhance and improve the SAVANNA model (including treatment of P-N interactions) and the parameterization and testing of the model using field measurements. Dr. Luanne Otter will coordinate collation and synthesis of data on savanna biogeochemistry and nitrogen cycles. Otter will also contribute to site-based and regional modeling with particular reference nitrogen biogeochemistry, trace gas emissions and comparison with measurements from the SAFARI-92 and SAFARI-2000 activities. Dr. Phil Omi will advise the other investigators, research associate and students on aspects of fire ecology and provide a liaison with research on fire behavior and biogeochemistry in north America and elsewhere. Dr. Gerhard Dangelmayr will coordinate with other project investigators and students on the mathematical abstraction of the ecosystem models. This will facilitate the formal analysis of non-linear parameter topology, ecosystem stability and transition likelihood. The research associate, to be employed full-time on this project under the direction of Hanan and Coughenour, will be responsible for regional and site-based simulations using the Savanna model and detailed analysis of the complex interactions and feedbacks between physical and biological variables that control ecosystem emergent properties.