**Biocomplexity in African Savannas – 2003 Progress Report**

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and participants in the workshop “African Savanna Complexity: different perspectives, common ground”.

**Abstract**

Savannas are globally important ecosystems of great significance to human welfare and economies, especially in many less developed countries in Africa and Eurasia. In Africa, the savannas are also home to the greatest density and diversity of large herbivores and carnivores of any ecosystem on earth. However, the mixture of trees and grasses that defines savanna systems
is inherently unstable and multiple factors related to soil type, climate, herbivore density, and wild-fire frequency are thought to contribute to their coexistence. Thus savannas are biocomplex systems where processes such as grazing intensity and fire frequency simultaneously depend on and control savanna structure, productivity and nutrient recycling.

This project is investigating biocomplexity in the context of African savannas. In our research we are investigating how complex interactions manifest themselves in the emergent characteristics of the diverse savanna regions around Africa, we are developing both conceptual and numerical models that will help us explain and analyze savanna dynamics, and new theory to explain how biogeochemistry, climate and disturbance interact and contribute to savanna dynamics across scales of space and time. The project will further use savanna systems as a general model for understanding complexity in biological systems and to develop methods of analysis and interpretive tools that promote a broader public understanding of the inter-relatedness of environmental systems.

Theories for the coexistence of trees and grasses in savanna systems have been divided between those that concentrate on competitive interactions and niche separation, and those that concentrate on temporal and spatial heterogeneities (broadly “disturbance”) that intermittently suppress or stimulate tree population growth. The review paper submitted to Ecology Letters take a broader, more integrated, look at the complex of factors controlling woody dynamics in savanna systems and proposes a comprehensive conceptual framework for understanding and studying savanna systems. Based on this framework we will be able to better understand the interactions and feedbacks that link climate, soil, fire and herbivory in controlling savanna structure and woody dynamics.

Two independent threads in this research project have provided strong evidence for the importance of a largely neglected process in savanna tree-grass interactions: intra-specific competition between trees controlling maximum tree cover in “mesic” savannas (200-600 mm annual rainfall). The first study grouped data on actual tree cover and basal area from several hundred sites in Africa which, when plotted against rainfall, show a distinct upper bound of tree cover. The second study examined tree cover in long-term fire exclosure plots in South Africa and showed the existence of a “thinning” line, indicating tree-tree competition for resources (presumably water). While tree-tree competition has been recognized from a conceptual point of view as a potentially important factor in savannas (and is ubiquitous in forest ecology), none of the existing numerical models that seek to explain tree-grass coexistence have included tree-tree competition as a factor structuring woody community density and canopy cover. The data gathered by this study strongly suggests that intra- as well as inter-specific competition may be important: full understanding of savanna complexity requires an integrated approach.

An additional contribution of this research is that, through the workshop series, we are providing a forum for a collaborative network of African savanna ecologists that will promote exchange of ideas and integrative studies within Africa, and between African ecologists and ecologists outside the region. It will further provide opportunities for ecological theory to contribute to, and benefit from, our understanding of ecosystem dynamics and biocomplexity as exemplified by Africa savanna systems.
Activities and Findings

Major research and educational activities

- The first workshop organized and funded by this project was held at Luiperdskloof Game Lodge, South Africa (January 23-25, 2003). The workshop, entitled “African Savanna Complexity: different perspectives, common ground” was attended by twenty-nine participants, including African savanna ecologists (21) and students from the University of Cape Town (5) and Colorado State University (3). Participants at the workshop work in east, west and southern Africa, with links to institutions in Africa, Europe and North America. Participants also included scientist from Kruger National Park Scientific Services. The workshop was held over three days, with keynote talks on the first day by Herbert Prins (Wageningen University), Pierre Hiernaux (University of Hohenheim, formerly ILRI-Niamey) and Peter Frost (University of Zimbabwe).

- Workshop participants contributed data from their research sites in Africa on savanna structure, climate, soils and disturbance regimes. Soils and dry-season plant samples from many of these sites were analyzed using common methodologies at Colorado State University. More sites have been added to the database from the literature and through personal contacts. The database now consists of more than 700 sites across Africa and provides an unprecedented resource for analysis of the patterns of savanna structure and how it varies across the continent.

- A post-doctoral research associate (Dr. Jayashree Ratnam) joined the project (January 2003) to develop and expand project studies on African savanna tree seed morphological adaptation, and biochemical-stoichiometric analysis of soils and plants, across gradients of climate and pedology. Both studies are aimed at developing theoretical understanding of how climate, chemistry, fires and herbivory contribute to tree community dynamics in savanna systems.

- Graduate students Bucini and Sea undertook exploratory fieldwork in the Kruger National Park, with measurements of tree community structure and demographics on the KNP Experimental Burn Plots. The EBP experiment has been run by the Park since 1955 and presents an excellent opportunity to investigate tree community response to differing fire regimes across rainfall and nutrient gradients. Initial results form this research are presented in the “Findings” section below.

- A technician (Ian McHugh) was employed for data collection and management associated with our intensive field site near Skukuza (the ‘tower site’) and soil and vegetation sample collection from a series of more than 100 locations in the Kruger National Park.

- The Kruger Park soil and vegetation samples have been analyzed at CSU for elemental contents (N, P K, Ca, etc.), soil textures and N-mineralization rates. These data will be used to investigate the nutrient stoichiometry and relationships with climate, soil and vegetation structure at high resolution across the classic savanna landscapes of the Kruger Park.

- Dr. Werner Kutsch secured independent funds to collaborate with the project, particularly on analysis of flux measurements from the tower site and to make more detailed

- Research associate Sankaran attended the Kruger National Park Science Network meeting, March 25-27, 2003 to present results from project meta-analyses and conceptual models of tree-grass coexistence in savanna systems.

- Climate data for Africa were used to estimate rainfall “modality”, and seasonality of precipitation with respect to temperatures. This will allow exploration of relationships between tree community dynamics and synchrony of rainfall with growing season. In many savanna systems around the world the timing of rainfall in winter and summer is crucial to the adaptive and morphological strategies employed by woody species. These data are available on the project website (http://nrel.colostate.edu/projects/bas/).

- Investigator Hanan organized a meeting of scientists with African research interests that took place during the IGBP-International Land Ecosystem Atmosphere Process Study (ILEAPS) meeting in Finland (October 2003). The African sub-meeting initiated a network (“Afriflux”) for collaboration and exchange between groups studying land surface-atmosphere exchange in Africa (including grassland, savanna and forest sites).

- Investigators Hanan and Scholes secured funding from IGBP-START for African scientist involvement in IGBP and Afriflux network activities. This included support for participation by 5 African scientists in the IGBP-ILEAPS meeting and Afriflux workshop in Finland, and will include intensive training during 2004 on micrometeorological methods in ecosystem research.

- An analysis of tree seed morphology has been initiated using data from the literature and new seed measurements to compare seed characteristics across contrasting climate and soils. These data will be used to examine adaptive strategies employed by species that are widespread in African savannas, with possible extension to analysis of germination and seedling characteristics in greenhouse experiments at CSU.

- The SAVANNA ecosystem model has been further developed during this year and applied to data from the Serengeti National Park, Tanzania

- Continental-scale datasets on tree canopy cover and climate are being explored to explore the emergent properties of savanna systems around Africa and how they relate to the primary climatic, edaphic and biological drivers

- The project website (http://nrel.colostate.edu/projects/bas/) was updated and maintained to provide descriptions of the research to the public, access to project plans and concepts to colleagues and access by collaborators to common datasets and results from meta-analyses

**Major findings**

1. Review and synthesis of mechanisms promoting tree-grass coexistence in savannas

A major theme in savanna research centers on the mechanisms that permit the coexistence of two distinct life-forms: trees and grasses in savannas. However, despite decades of research, a
consensus on the mechanisms permitting coexistence remains elusive. One major focus of our work this year involved revisiting the assumptions and predictions of extant models of savanna dynamics, attempting to reconcile their differences, and developing a conceptual framework that integrates existing approaches and applies them explicitly to different life-history stage of trees (Sankaran et al., 2003, in review). Broadly, explanations for the persistence of tree-grass mixtures in savannas fall into two categories that either concentrate on resource-based mechanisms, where niche separation and competition for limiting resources such as water lead to tree-grass coexistence, or disturbance-based mechanisms, where coexistence is promoted by factors such as fire, herbivory, rainfall variability, or other forms of spatial and temporal heterogeneity (Figure 1). Tests of these models have been largely site-specific, and although different models find support in empirical data from some savanna sites, enough dissenting evidence exists to question their validity as ubiquitous mechanisms of tree-grass coexistence. The lack of consensus on determinants of savanna structure and function arises because different models: i) focus on different demographic stages of trees, ii) focus on different limiting factors of tree establishment, and iii) emphasize different subsets of the potential interactions between trees and grasses.

Furthermore, models differ in terms of the most basic assumptions as to whether trees or grasses are the better competitors, and also make different predictions regarding how tree grass ratios should change across gradients of rainfall. We believe an integration of competition-based and disturbance-based approaches is required if a comprehensive model that explains both coexistence and the relative productivity of the tree and grass components across the diverse savannas of the world is to emerge (Figure 2). We synthesize the major findings of this work and outline a conceptual framework that integrates existing approaches in a review paper that has been submitted to, and is in review by, a leading ecological journal, *Ecology Letters*.

2. Continental scale patterns in savanna structure

Although woody cover in savannas is dynamic, savanna systems are in general persistent over time. Resource availability (water, nutrients), fire and herbivory are all thought to exert important regulatory influences, but perceptions differ on which combinations of these factors are the primary drivers of savanna structure. In part, this lack of consensus arises because most studies have been small-scale and site-specific, and it is likely that different factors may be active to different degrees in different savannas of the world. To investigate how the relative importance of these different factors varies across broad environmental gradients, we carried out a meta-analysis of savanna structure based on data from 176 sites in Africa. Tree cover ranged from 0-90% across sites and increased with rainfall, but between 200-600mm rainfall an upper bound on maximum tree cover exists that correlates with annual rainfall (Figure 3). This bound on tree cover exists despite inclusion of sites with low-fire frequency (Figure 4a), and low herbivore populations (Figure 4b), and is not related in any consistent way to either soil nutrient status or soil texture (data not shown).

The data provide strong evidence for intra-specific competition between trees for water: a mechanism for savanna persistence not frequently invoked. The results further suggest that savannas switch from being water-limited equilibrium systems to disturbance-mediated non-equilibrium systems across a gradient of increasing rainfall. Between about 200-600 mm, water availability limits tree cover and permits grasses to persist in the system. In this range of rainfall,
fire and grazing, although capable of modifying tree-grass ratios, are not necessary for tree-grass coexistence. Above 600mm rainfall, water availability appears sufficient to support tree canopy closure such that grasses can be out-competed. Savanna systems in this range of rainfall represent disequilibrium systems where disturbances such as fire, grazing and browsing maintain tree-grass co-existence by preventing tree canopy closure.

3. Linkages between N & P availability and savanna structure and dynamics

We have also developed analytical and spatial models that explicitly link savanna structure and function to the availability of limiting soil nutrients (N & P) and moisture (Figure 5). The model describes the change in ecosystem carbon, nitrogen and phosphorus through time based on the mass balance of the system and the diverse loss and gain vectors associated with each chemical species. Herbivory and fire are also simulated, based on nutrient status of the vegetation, fuel load and climate. Based on this new model, we simulated long-term dynamics of carbon, nitrogen and herbivore consumption across the African continent. Preliminary results indicate that the model is able to predict patterns of aboveground carbon and nitrogen stocks and herbivore consumption levels with reasonable fidelity, suggesting the model captures most of the essential dynamics of nutrients and herbivory at the continental scale. This model will be further developed and used to investigate the interactions and feedbacks between savanna structure, climate, fire, herbivory and nutrient deposition and loss pathways.

4. “Thinning” relationships in savannas

The relationship between average tree size and density has often been studied in forest systems to better understand the effects of resource limitation. In particular in managed forests approaching canopy closure, there is a predictable decline in tree density (through mortality) as the trees continue to grow. This phenomenon has become known as the thinning law. However, thinning law concepts have not frequently been investigated in savannas, in part because “thinning” implies the existence of intra-specific (tree-tree) competition and savanna ecologists have tended to focus on inter-specific (tree-grass) competition and disturbance as the primary factors promoting savanna persistence. The purpose of this work was to critically examine whether thinning law processes may, in fact, apply to savanna ecosystems.

A pilot study was carried out using the long term experimental burn plots (EBP) established in the mid-1950’s by scientists of the Kruger National Park, South Africa. The EBP include replicated experimental treatments located in four contrasting vegetation types across the gradient of rainfall available in the Park (350-750 mm). For this study, tree size and density measurements were made on the control plots on which one of the primary disturbance factors (fire) has been suppressed for almost 50 years (Figure 6). In these savanna plots, with long-term fire suppression, the density-basal area relationships appear to converge with a slope that is close to the empirically and theoretically expected slope of -1.0. These results suggest that in savannas, which are water-limited environments, tree on tree competition for water does occur. Furthermore, it provides a mechanism for maintenance of savannas that does not require either disturbance or tree-grass competition to explain tree and grass coexistence in savanna systems.
5. Geographic variation in seed traits of African savanna tree species: a macro-ecological study

This part of our work on complexity in African savannas explores patterns and environmental correlates of variation in seed traits of common African savanna tree species, and aims to interpret these in the context of selective forces that are thought to be important drivers in savanna systems. We reason that selective regimes across broad environmental gradients will be reflected not only in the structure and functioning of savannas (as in Figure 3), but also in the physiology and morphology of savanna species. To explore these ideas, we selected candidate tree species that are representative of savanna habitats and have geographic ranges that extend across the African continent, such that different populations sample different rainfall, nutrient, fire and herbivory regimes. Using these criteria, we selected five species of the common African savanna genus *Acacia*: *Acacia albida* (now *Faidherbia albida*), *Acacia tortilis*, *Acacia nilotica*, *Acacia Senegal* and *Acacia erioloba*.

Since much empirical evidence suggests that seed and seedling life-history stages are critical bottlenecks in many savannas, we have focused our attention on geographic variation in these life-history stages that are expected to be under heavy selection pressure. Seed traits that are known to influence seed germination and seedling establishment include seed mass, seed dimensions and seed endosperm-coat ratios. Preliminary analyses on data from 70 populations of *F.albida* from across the African continent (data compiled from the literature) reveal a directional latitudinal trend in mean seed mass across populations of this species. From northern to southern latitudes in Africa, seed mass increases linearly (Figure 7). A multiple regression analysis of environmental correlates explained 69.8% of between-population variation in mean seed mass with mean annual temperatures, mean annual rainfall and percent tree cover (perhaps correlated with shading of seeds and seedlings) having significant effects on population mean seed mass. Mean seed mass decreased in areas with high rainfall and high temperatures, but increased in areas with high tree cover (Figure 8). These trends are consistent with expectations of environmental effects on maternal investment in seed traits that maximize germination success in a given habitat (e.g., seedlings from larger seeds are more shade tolerant and survive better in more competitive habitats).

We are currently in the process of obtaining seed lots from seed centers around the world to expand these analyses to all target *Acacia* species. If, as we expect, these trends are borne out across all *Acacia* species, and seed traits are predictably relatable to seed germination and establishment success, we will a) demonstrate that factors considered important drivers of emergent savanna properties such as vegetation structure are also drivers of morphological traits in savanna trees and b) add a new dimension to the consideration of savanna structure and function through a consideration of constraints on seed production, a critical demographic variable in savanna tree species (Figure 2).

**Project Issues in the Kruger National Park**

The Biocomplexity in African Savannas project is studying savanna systems across Africa to compare how vegetation structure changes across the large gradients and discontinuities of climate, soil, land use and management. However, several studies are concentrated in the Kruger National Park because of the great climatic diversity of the Park, because of the excellent long-term and on-going research of KNP scientists, and because of the availability of the Skukuza
tower site and established scientific relationships. Our working relationship with KNP Scientific Services has been excellent: during the last year we have continued and expanded efforts at the Skukuza tower site, and sampled vegetation and soil extensively around the Park in collaboration with Dr. Grant. We also initiated work on the EBPs with very encouraging early results (reported above; Figure 6) that we would like to build on. However, we did run into controversy with our colleagues from the University of Cape Town, due largely to our misunderstanding of their existing activities. We therefore adjusted our research plans for the EBPs to avoid this clash, and have initiated discussions with UCT to see if our revised plans are acceptable to them. We hope that in the coming months we will be able to move ahead with more extensive ‘thinning’ analyses in collaboration with both KNP Scientific Services and UCT.

Future Research in the Kruger National Park

In the coming year we would like to continue our work at the flux tower, concentrating in particular on analysis of the several years of carbon dioxide, water and energy fluxes over Combretum and Acacia savannas. These analyses are now progressing well and we expect to submit papers before the end of the year. The analysis of plant and soil samples from sites around KNP is now completed and we plan to work up results and initial interpretations, in collaboration with Dr. Grant and other KNP scientists, in time for the Kruger Park Scientific Network meeting in March 2004. We also hope to collaborate further with KNP Scientific Services (Andre Potgeiter and Navashni Govender) on analysis of EBP woody community structure to expand the ‘thinning’ analyses. The EBP work-plans are subject successful negotiation with UCT colleagues and registration of the sub-project with Scientific Services.

Publications and Products

1. Journal and Book Publications
Publications by project investigators partially or wholly supported by BAS (project participants in bold)


2. Presentations


_Plant diameter distributions in Kruger National Park, South Africa_ (Gabriela Bucini, William Sea, Niall Hanan), Presentation at the Front Range Student Ecology Symposium, Fort Collins, CO, April 2, 2003

_An Ecological Thinning Law Applied to Trees in Kruger National Park, South Africa_ (William Sea, Gabriela Bucini, Niall Hanan), Presentation at the Front Range Student Ecology Symposium, Fort Collins, CO, April 2, 2003

_An Introduction to Biocomplexity_, (Niall Hanan), Colorado State University Undergraduate Introduction to Ecology, April 23, 2003


_Vegetation structure in African savannas: continental-scale patterns suggest equilibrium, and disequilibrium dynamics_, (Niall Hanan, Mahesh Sankaran, Jayashree Ratnam), Poster presentation at the National Science Foundation BE-PI workshop, Arlington, VA, September 14-17, 2003.

3. Other Products

The project website at [http://www.nrel.colostate.edu/projects/bas](http://www.nrel.colostate.edu/projects/bas) provides details to the general public and the scientific community on the concepts, aims and progress of the project. The Graduate seminar on biocomplexity was also made available ([http://www.cnr.colostate.edu/class_info/ey592](http://www.cnr.colostate.edu/class_info/ey592)). Links to third party publications are password protected for copyright reasons.
Through collaboration with scientists working at a large number of sites in east, west and southern Africa, we have collected data from a large number (>700) savanna field sites on savanna structure with ancillary information on climate, soils, herbivory and fire regimes, and management practices. Plant and soil samples from a large subset (>100) sites have been analyzed for texture, total nitrogen and phosphorus, and N-mineralization rate. The resulting database forms the basis for extensive meta-analyses that are in progress in collaboration with participants of the African Savanna Complexity workshop.

A more spatially-intensive study has collected soil and vegetation samples from over 100 locations in the Kruger Park which are being analyzed in the same way as the continental-scale samples. These will be used to investigate local scale patterns that respond to the rainfall gradient in the Kruger Park (350-750 mm) and the divergent nutrient-rich and nutrient-poor soils on basalt and granite derived soils, respectively. These data will be analyzed in collaboration with scientists from the Kruger National Park Scientific Services (Dr. Rina Grant).

Opportunities for training and development

The workshop held in January 2003 in South Africa, and subsequent workshops planned in later years in east and west Africa, provide opportunities for additional students, particularly students from Africa, to attend the meetings, interact with prominent African savanna ecologists, and contribute their ideas. African student participation will be possible in part through NSF support, as well as from local resources.

Separate support for training of young African scientists in ecosystem research has been obtained from the International Geosphere-Biosphere Program (IGBP) System for Technology and Research Training (START). These funds have supported participation by 5 African scientists in the early days of IGBP reorganization and the initiation of the AfriFlux network. It will further support intensive training in micrometeorological field techniques during a workshop scheduled for April 2004 in the Kruger National Park, South Africa.

The NSF Biocomplexity in African Savannas project has provided support for three graduate students at PhD level and training of two undergraduate students in laboratory and data analysis. Two graduate students (Gabriela Bucini and William Sea) began at CSU in Summer 2002 to work on different aspects of savanna complexity. A third graduate student (Gericke Sommerville) is being provided partial support in the final stages of her research on herbivore impacts on savanna structure in the Serengeti National Park, Tanzania. Two undergraduate students (Anita Lahey and Jenna Rettenmayer) have been employed on the project to work on data analysis and laboratory analysis of plants and soils from African savanna sites.

We also led a Graduate Seminar entitled “What in the World is Biocomplexity: an investigation of complexity in environmental systems” that was attended by graduate students and interested faculty members. The Seminar series was developed with a web page (http://www.cnr.colostate.edu/class_info/ey592), guest lecturers and literature discussions and was well received.
Figure 1. Predicted tree-grass ratios across rainfall gradients (a) spatial niche-separation model, (b) balanced competition model, and (c) disturbance-based models. Solid lines show expected tree cover in the absence of external perturbations. Arrows indicate potential effects of disturbances on tree cover.
Figure 2. Framework that integrates demographic and competitive approaches to tree-grass coexistence issues in savannas. Demography is included in the form of four recruitment rates that express transitions between relevant life-history stages of the tree. All interactions are embedded within an overarching environmental context (rainfall, soil texture and nutrient status), which ultimately regulates the recruitment and competitive indices shown.
Figure 3. Tree cover response to rainfall across 176 African savanna sites collected for the African Savanna Complexity Workshop (organized and funded by this project). Colored symbols indicate sites in west, east and southern Africa.

Figure 4. Tree cover response to rainfall in African savannas with (a) separation between sites with high fire frequency (< 3 yrs; red) and low fire frequency (> 3 yrs; black) and (b) separation between sites with high herbivore biomass (>3000 kg/ha; red) and low herbivore biomass (< 3000 kg/ha; black). Data are as in Figure 3 but for the reduced sets for which fire/herbivory data were reported.
Figure 5. Simulation of above-ground carbon (C) and nitrogen (N) stocks in African ecosystems, and fraction of annual net primary production consumed by herbivores (%). These model simulations were produced using a simple model of carbon, nitrogen and phosphorus mass balance and palatability of biomass to large herbivores.
Figure 6. Mean basal area plotted against plot density (log-log scale) in control (unburned) Experimental Burn Plots (EBP) in three locations in the Kruger National Park, South Africa. A least squares fit determined a slope of –1.09, which agrees reasonably well with published work and theoretical predictions of Enquist and Niklas (2001).
Figure 7. Mean seed mass in populations of *Faidherbia albida* (formerly *Acacia albida*) increases towards southern latitudes.

Figure 8. Preliminary data on the effect of environmental variables on mean seed mass in *F. albida* suggest the potential for multiple environmental constraints on seed traits.