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DISSERTATION

THE SERENGETI ECOSYSTEM: SPECIES RICHNESS PATTERNS, GRAZING, AND LAND-USE

Submitted by

Kristine L. Metzger

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

for the Degree of Doctorate of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2002

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY KRISTINE L. METZGER ENTITLED "THE SERENGETI ECOSYSTEM: SPECIES RICHNESS PATTERNS, GRAZING, AND LAND-USE" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS OF THE DEGREE OF DOCTORATE OF PHILOSPHY.

<u>Committee on Graduate Work</u>

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ABSTRACT OF DISSERTATION

THE SERENGETI ECOSYSTEM: SPECIES RICHNESS PATTERNS, GRAZING, AND LAND-USE

The Serengeti National Park is a natural laboratory for many reasons, particularly because it is a large, continuous stretch of land that harbors very diverse and dense biological fauna that has not been modified through human-induced changes. The ecosystem spans a precipitation, nutrient availability, and productivity gradient and is contained within areas managed under different land use practices.

Using a multi-scale plot design, vegetation species richness was sampled along this gradient to determine the relationships between species richness, primary productivity and scale. It was found that species richness was positively correlated with water availability and primary production and negatively correlated with nutrient availability. Examination of the slopes of the species area curves for each plot determined that species richness accumulated at a faster rate with increased water availability and primary production. Species richness was lowest in areas with limited water availability and heavy grazing and increased when released from these constraints.

The short-grass plains, which are critical habitat for the wildebeest migration, falls into two land use areas, the Serengeti National Park (SNP) and Ngorongoro Conservation Area (NCA). The SNP is a nature reserve while the NCA is a multi-use area allowing settlement and livestock grazing. This study examines vegetation structure and diversity patterns on the short-grass plains where changes in land-use have resulted in a portion of the plains that is grazed historically only during the wet season but is now grazed throughout the year by livestock. Vegetation diversity was not found to be different between these two areas, but changes in vegetation structure were correlated to dry season grazing densities, indicating that changes in the season of grazing could be influencing vegetation structure.

Woody vegetation structure and woody species composition is described along the precipitation gradient. Below approximately 500 mm mean annual precipitation, woody species are essentially absent from the landscape and herbaceous vegetation coverage is high. Above this threshold, woody species begin to appear on the landscape. As precipitation increases, density of trees increase and trees become taller. This increase in woody species is accompanied by a decrease in herbaceous vegetation coverage. Species composition is also described. The family Fabaceae is the most dominant species of trees under 900 mm mean annual precipitation, but above 900 mm of rainfall four families are equally represented.

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This dissertation was a team effort. Even though I am getting credit for writing it and putting it together, it would not be possible with out the help of so many people. In many ways, I don't want sole credit for it because it was a group effort and I feel that the dissertation process does a disservice to scientists by portraying the dissertation as a culmination of one individual's ideas, experiments and results. To me, science at its best is a group endeavor; ideas stemmed though cooperating and collaborating, experiments developed through consulting and critiquing, results generated by discussing and sharing. Even though much of this project has been a group effort, much of the final production has been an individual effort. I have enjoyed every step of this process from conception to completion. To many people, too many to list, I give thanks for helping and contributing to this project in diverse and multiple ways.

First I would like to thank my committee. My advisors, Drs. Robin Reich and Mike Coughenour have been incredibly supportive and helpful through this entire process, both of whom live incredibly busy lives but they were always very quick to answer all of my questions. Both have made enormous contributions to this project through thoughtful discussions and genuine interest and concern for the outcome of the project and for my personal development as a scientist. The opportunity to live and work in the Serengeti and East Africa was an unbelievable experience. It was by far the most amazing thing I have ever done and I am so thankful to my advisor, Mike, for believing in me and having the confidence in me to deal with life in the bush. It was an experience of a lifetime. I will treasure it forever. I would like to show my appreciation for Duane Boes for being the most incredible teacher I have ever had (and I have taken a lot of classes through the years). He showed incredible patience and an amazing willingness to go above and beyond his obligations as a teacher in order to dumb-down statistics to a level I could understand. His retirement is a huge loss for the statistics department. It is unusual that someone can be so good at teaching such a difficult subject matter. Finally, I thank Tom Stohlgren, for always being incredibly supportive and having positive things to say and such innovative ideas on ecology.

Extra special thanks go to: Michael Anderson for sharing his data, ideas, and enthusiasm for ecology, Dave Raff for having the compunction to find solutions to problems even when it is clearly not worth his time, Jonathan Straube for listening to me 'freak' out and spending his free time to help me with my constant computer problems, Rebecca McCulley for being a good friend and knowledgeable biogeochemist, Randy Boone for always taking the time to answer what seemed like weekly phone calls with questions, Tony Sinclair for spending days of his precious field work time to help me identify Acacias and develop a reasonable sample design in the Serengeti, Rick Shory for introducing me to the wonderful world of database management, Emilion Peters for teaching me have to deal with life in the bush, Denne Reed for technical support in the field, Tony Cheng and Nicole DeCrappeo for moral support and comic relief and Peter Adler for being a great editor and always being open to discussing ecology, especially when it involves grazing. Each of these people have made a substantial contribution to this project, all in very different ways.

Words cannot express my gratitude for the support and encouragement I have received from my parents, without their love and support I would never have had the confidence to pursue such a daunting endeavor.

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INTRODUCTION

The Serengeti can be considered a natural laboratory for many reasons. The Serengeti ecosystem is a large, continuous stretch of land which spans a natural precipitation and productivity gradient that harbors very diverse and dense biological fauna. In addition, the system has not been modified through human-induced changes in land-use or over-exploitation. Limited water availability has made cultivation difficult and infestation of the disease carrying tsetse fly excluded much of the system from prolonged livestock grazing, inhibiting settlement throughout the park. The boundaries of the ecosystem were designed to maintain the seasonal migration of the 1.5 million wildebeest that graze this system heavily every year.

Research in the Serengeti ecosystem has been ongoing for over four decades. This research has been a joint effort, involving teams from all over the world asking basic to applied questions to develop a better understand of how this system works in order to effectively manage this very valuable world treasure while simultaneously contributing research findings to the scientific world as a whole. This research has had an enormous impact on the way ecologists view biodiversity, ecosystem functioning, herbivore-plant interactions and grazed ecosystems.

Ecology is using a more integrative approach to examining ecosystems structure by asking questions about species interaction with ecosystem processes over many spatial scales as apposed to the traditional individual species approach. This integrative approach includes taking into consideration the natural history, abiotic and biotic inputs and outputs, species-ecosystem interactions of the system and the contingent conditions that all of these forces may be contributing to the patterns and process we are seeing today. The research contained in this dissertation addresses basic to theoretical questions while attempting to incorporate previous research findings and data from past research projects.

My field work was focused in both the Serengeti National Park and Ngorongoro Conservation Area. The adjacent NCA is managed very differently than the SNP. The SNP is a true nature preserve; human habitation is limited to park personnel, researchers, and staff that run the tourist concessions. Ngorongoro Conservation Area is managed under a multi-use designation which allows settlement and livestock grazing in the conservation area. Ngorongoro Conservation Area and SNP share one of the most valuable resources for the wildebeest migration, the short grass plains. The wildebeest migration travels to the plains each year during the wet season to graze on the very nutritious short grasses of the plains and calve their young. This area is historically grazed only during the wet season and rested during the dry season when the migration leaves the plains and travels north in search of forage and water. With the introduction of Maasai to the area, the plains are now grazed during the dry season in many areas. I was interested at looking at vegetation structural and diversity differences between these two area, the area that occurs on the plains within the SNP and is still only grazed during the wet season by the native ungulates and the adjacent area, NCA which is now grazed through out the year by both wildebeest (during the wet season) and livestock (dry season grazing). In addition, the spatial distribution of grazing ungulates changes seasonal, so the question of whether differences in diversity or vegetation structure were found with the different grazer densities at different times of the year was also addressed.

Theoretical questions were addressed regarding species richness patterns at different scales along the precipitation and productively gradient in this system. This was a collaborative effort with Michael Anderson of Syracuse University who collected over half of the labor intensive Modified Whittaker plots. We were interested in determining the role that environmental and nutrient availability constraints had on the species richness patterns at different scales of measurement.

Chapter three is a descriptive snap shot of the savanna vegetation structure along the precipitation gradient in this dynamic system. Tree regeneration can be very rapid in the Serengeti, often times trees can disappear and regenerate within 50 years. Basic descriptive information is still essential for researchers to understand drivers of vegetation dynamics in this system. I examined the woody vegetation structure in terms of tree density, height, and composition along the precipitation gradient in relation with herbaceous vegetation cover.

Chapter one is focused on an applied research question looking at the potential influence of changing grazing strategy on the vegetation structure in a system that is historically grazed during the wet season but because of changes in land use it is now grazed during the dry season. The second chapter is asking theoretical questions about how species richness patterns are influenced by ecosystem variables across the very pronounced precipitation gradient in the Serengeti and how these species richness patterns change over space. Chapter three examines the structural relationships between the herbaceous vegetation cover and woody species.

This dissertation uses an integration of data collected or compiled by me, Michael Anderson (Syracuse University, Syracuse, NY), Sam McNaughton (Syracuse University, Syracuse, NY), Roger Ruess(University of Alaska, Fairbanks, AK), Ken Campbell (Natural Resource Institute, Kent, UK., Brian Farm (USGS, Hilo, HI), Randy Boone (Natural Resource Ecology Laboratory, Fort Collins, CO), Denne Reed (SUNY-Stony Brook, NY), Serengeti Ecological Monitoring Program (Serengeti National Park Tanzania), Tanzania Wildlife Research Institute (Arusha, Tanzania), Tanzania National

Parks (Arusha, Tanzania), and the Frankfurt Zoological Society (Frankfurt, Germany).

CHAPTER I: EFFECTS OF THE SEASONALITY OF GRAZING ON VEGETATION DIVERSITY, COMPOSITION, AND STRUCTURE IN A SEMI-ARID ECOSYSTEM OF EAST AFRICA

1.0 Abstract

The Serengeti ecosystem located in Tanzania, East Africa, spans a number of different land use areas ranging from true nature reserves to areas where land use is completely unrestricted. Concern has been raised about the effect that land use change may have on diversity and vegetation composition and structure. To address this concern, this study focuses on the two main areas that comprise the heart of the short-grass plains of the Serengeti ecosystem, the Serengeti National Park (SNP) and Ngorongoro Conservation Area (NCA). The Serengeti National Park is a true nature reserve and the adjacent area, NCA is a multi-use area, defined by the allowance of livestock grazing by the indigenous Maasai pastoralists. The introduction of livestock to the short-grass plains within the NCA borders has imposed land use change in two ways: it has increased animal densities throughout the year and has modified the natural grazing regime in that livestock graze during the dry season while wildlife only graze during the wet season.

The objectives of this study were to: 1) determine if diversity and vegetation structural differences exist between areas that have been historically grazed only during the wet season and areas that are now grazed during both the wet and the dry season; 2) determine if significant correlations existed between vegetation diversity and structure with density of animals during the wet and the dry seasons. A spatial autoregressive model was used to evaluate differences between the two area and if vegetation structural differences were correlated to grazer densities. There were no significant differences in plant species H' diversity, evenness, richness, or vegetation structure found between the two land-use areas. However, density of grazers during the dry season was positively correlated with relative abundance of forb and shrubs and cover of shrubs and bare ground while being negatively correlated with grass cover. Although no difference in plant diversity was found between the two areas under different grazing regimes, the correlation between density of dry season grazers and vegetation structure could indicate that changes in the seasonality of grazing may be altering vegetation structure and relative abundance of plant functional types.

1.1 Introduction

The Serengeti ecosystem is functionally defined by the seasonal migration of over 1.5 million wildebeest. The ecosystem spans political boundaries and includes administrative units having a variety of different land-use designations (Figure 1-1). Despite the different management strategies and land-use practices amongst these areas, all share a common mandate which places a high priority on the conservation of biodiversity. Grazing induced land-use changes have the potential to alter vegetation composition to either less productive species (Chapin III et al. 1997) or less palatable species (Moretto and Distel 1999), and can negatively impact available forage. Changes in vegetation composition and structure can have very important consequences for influencing suitable habitat for livestock and wildlife. Therefore it is important to examine potential effects of land use change on vegetation diversity, composition and structure.

The Serengeti National Park is the most well known component of this ecosystem. It is a nature reserve and managed as such; human habitation is restricted to national park personnel and no hunting or grazing by domesticated livestock is allowed within the park boundaries. Adjacent to the SNP is Ngorongoro Conservation Area (NCA). Ngorongoro Conservation Area is considered a buffer zone for the ecosystem and is small in size compared to SNP (9,000 km^2 compared to 17,000 km^2). Ngorongoro Conservation Area is designated as a World Heritage Site and this designation targets the preservation of both cultural and natural world treasures. The multi-use status is based on the premise that the indigenous people, Maasai, can successfully coexist with the wildlife populations. Maasai are pastoralists and their livelihood and culture depend on the herding and maintenance of cattle. This reliance on cattle for sustenance coupled with a cultural ban on the use of wildlife for food fosters coexistence of natural wildlife populations while

Figure 1-1. The Serengeti ecosystem and different land-use areas.

providing an area where Maasai can live much as they have for hundreds of years. The portion of the Serengeti ecosystem that falls within the NCA border (the short-grass plains) is small in area but its importance to the system is critical. The short-grass plains habitat is essential wet season grazing and calving grounds for the migratory wildebeest population.

The multi-use designation in NCA has come under attack in recent years by conservationists concerned that the mandate for the preservation for biodiversity is not being achieved. Advances in health and veterinary care, and immigration from surrounding areas have led to a dramatic increase in the human population (3%/year; Parkipuny 1997). This increase in human population is accompanied by more reliance on small-scale cultivation (< 0.4 ha/family) which has resulted in a more sedentary lifestyle than is usually associated with the pastoralist tradition (Parkipuny 1997). Conservationists are concerned that this increase in human population and the switch to a more sedentary lifestyle will lead to increased cultivation, exclusion of wildlife from grazing areas, and an overall degradation of habitat driven by livestock grazing. All these factors, conservationists believe, will eventually result in a loss of important fauna. Although, this concern has been addressed by past studies that have demonstrated the resilience of the plains and have failed to detect any evidence of degradation (Sinclair 1995, Misana 1997, Ward et al. 1998); little work has been done on the influence livestock grazing has had on the structure of the vegetation and the diversity of plant species.

Livestock grazing can have impacts on biodiversity and vegetation composition and structure. This impact varies greatly between different ecosystems (Schlesinger et al. 1990 Milchunas and Lauenroth 1993). Semi-arid ecosystems that have long evolutionary histories of grazing have been shown to be resilient to impacts of livestock grazing, and the vegetation community has been shown to be insensitive to the replacement of native grazers and browsers by domesticated animals (Milchunas et al. 1989). In many semi-arid grassland ecosystems, inter-annual productivity and species composition changes are thought to be much more sensitive to stochastic rainfall events than to heavy grazing and high stocking densities (Ellis and Swift 1988, Dahlberg 2000). Yet, in many ecosystems, grazing undeniably alters vegetation structure and ecosystem functioning. Grazing has been shown to increase heterogeneity of landscapes (McNaughton 1985, Belsky 1992), abundance of forbs, rates of nutrient cycling (Ritchie et al. 1995), vegetation productivity (Pimm 1984,Vitousek et al. 1997), and can lead to increases and decreases in biodiversity (Shackelton et al. 2000, Dahlberg 2000). Grazing has also been identified as causing increased soil erosion (Khresat et al.1998), shrub and exotic species invasion (Manzano and Navar 2000), and as having negative impacts on other fauna distribution and abundance (Eccard et al. 2000). Changes in species composition have been identified through selective grazing pressures which have led to increased densities of unpalatable grasses (Moretto and Distel 1999). Results of changes in land use practice, including grazing, often lead to changes in biodiversity (Mooney et al. 1996, Chapin III et al. 1997, Vitousek et al. 1997) and vegetation structure (Noy-Meir 1979, Walker and Noy-Meir 1982, Noy-Meir 1993).

In arid to semi-arid ecosystems with long evolutionary histories of grazing spanning thousands of years, the vegetation has adapted to grazing and drought through a variety of strategies. These ecosystems are dominated by species that possess traits, such as small stature, high shoot densities, high shoot turnover and rapid growth, and are able to tolerate or avoid grazing and drought (Coughenour 1985). Other ecosystems that have long evolutionary histories of grazing and are dominated by grazing tolerant species have been shown to be modified through land use changes such as changes in the natural grazing regime, or changes in the timing of grazing (Eckert and Spencer 1987, Bork et al. 1998). These modifications have been manifested through changes in species composition and vegetation structure (Weber et al. 1998). Thus, alterations in the grazing regime could potentially be influencing the composition, structure, and diversity of the vegetation in the Serengeti ecosystem.

The Serengeti ecosystem has a very long evolutionary history of grazing and has highly variable rainfall patterns. The short-grass plains experience a burst of growth during the short growing season (January-May). The yearly arrival of the wildebeest migration on the short-grass plains and their yearly synchronized calving is timed with the wet season rains. The arrival of the wildebeest precludes Maasai cattle from using the short-grass plains during the wet season due to a fatal disease, Bovine Malignant Catarrh Fever, that wildebeest carry but are not affected by. Therefore, during the wet season, the short-grass plains are grazed exclusively by the wildebeest. With the onset of the dry season, the grass senesces and the wildebeest leave the plains and travel to the northern part of the park where annual rainfall is greater, and the growing season is longer. The dormant grasses of the short-grass plains within the SNP are essentially untouched until the wildebeest return the following year for the next growing season. Because of the multi-use designation that is within the NCA boundary and on the short-grass plains, once the wildebeest leave the short-grass plains, Maasai livestock graze the portion of the short-grass plains that is within the NCA boundary during the dry season, altering historical animal densities spatially and temporally (Machange 1997) prior to Maasai occupation. This alteration in land use practice from the state that plant species evolved under could affect the diversity and structure of the vegetation.

This study addresses several questions. Are differences detected in vegetation diversity and structure between one area that is grazed only during the wet season and the adjacent area which is grazed both during the wet and dry season? Are differences in vegetation structure and diversity strongly correlated with differences in grazing pressure, spatially and temporally? These questions are addressed through analyses of vegetation diversity and structure, and comparisons of grazing pressure between the nature reserve (SNP) and the multi-use area (NCA). Although the comparative rather than the controlled experimental nature of this study can not answer this question directly, it can quantify and identify differences between the areas under different grazing densities, temporally and spatially.

1.3 Methods

1.3.1 Site Description

This research was conducted on the short-grass plains of Serengeti ecosystem, Tanzania, East Africa. The mean annual precipitation and temperature for the region is approximately 500 mm and 22° C, respectively. The terrain is flat to gently undulating. Short stature C4 grasses dominate. Soils are mainly Calculastolls.

Sites (Figure 1-2) were stratified by grazing regime zones. Areas of different grazing regimes were identified from a regional analysis of the seasonal movements of

Maasai livestock (Parkipuny 1997).

1.3.2 Vegetation Sampling

Diversity was measured using a modified-Whittaker plot design (Stohlgren et al. 1995). The modified-Whittaker is a multi-scale design covering a total area of 1000 m^2. Nested within the 1000 m^2 plot are ten 0.5 x 2 m (1-m^2) subplots, two 2 x 5 m (10-m^2) at opposite corners, and a 5 x 20 m (100-m^2) at the plot's center. In the 1-m^2 subplots, all species were identified and percent cover and height by species was recorded. Twelve modified-Whittaker plots were established: five in SNP and seven in NCA. Species presence was recorded at the other scales within the plot. Diversity and evenness were calculated using the Shannon index of diversity (H' diversity) using a log base 10. Landscape level diversity was analyzed using the Jaccard's coefficient which determines the degree of similarity between species lists. Jaccard's coefficient was used to quantify plant species overlap within and between the SNP and NCA. Jaccard's coefficient is defined as:

$$J = A / (A + B + C)$$

A = the number of species that are identified in an area, B= species found in area 1 and absent from area 2, and C = species present in area 2 but not area 1. Jaccard's coefficient measures the biological similarity of species richness between two plots by determining

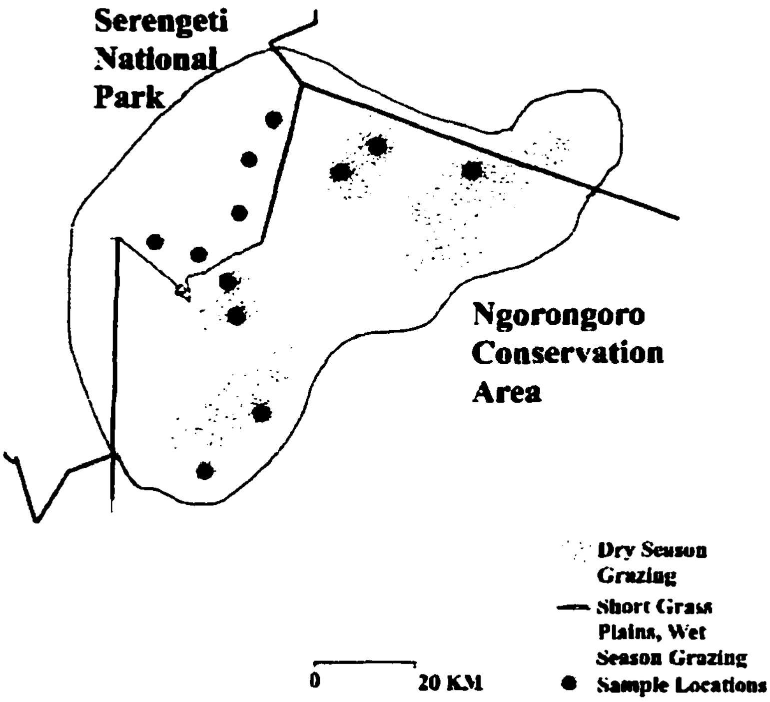

Figure 1-2. The Serengeti plains and different grazing zones.

the proportion of combined species richness shared between plots. Complete overlap between two species lists generated from sampling produces a coefficient of 1.0, while no overlap generates a coefficient equal to 0.0.

The functional composition and structure of the vegetation was measured by using two 5-km perpendicular transects. At 1-km intervals, nine 8-m radius plots were established. The 9 plots were systematically laid out on a 30 x 30-m grid (Figure 1-3), 1,053 8 m^2 plots in total. Coarser scale information that captured the vegetation structure was recorded in these 9-point plots including cover and height of forbs, grasses, shrubs, and bare ground, as well as identity of dominant grass species. The vegetation composition was determined using two different methods: raw cover data and relative abundance of functional types.

1.3.3 Grazer Density Distributions

Grazing pressure was estimated from density distributions of native ungulates and domesticated livestock generated by the SAVANNA ecosystem model (Boone et al. 2001). The model of livestock distributions was parameterized based upon 1999 aerial and ground surveys conducted by the Ngorongoro Conservation Area (NCAA ecological monitoring program) while the model of native ungulate distributions was parameterized using data from aerial surveys (Campbell and Borner 1995). Movements of animals were predicted based on the distributions of influencing factors such as distance to water, topography and forage biomass. All animal densities were converted to tropical livestock units (TLU's) per km^2, which is the equivalent of one 250 kilogram animal, per km^2. Three years of model output were generated on a monthly time step and animal numbers were averaged over seasons to estimate grazing pressure distributions during the wet and the dry seasons.

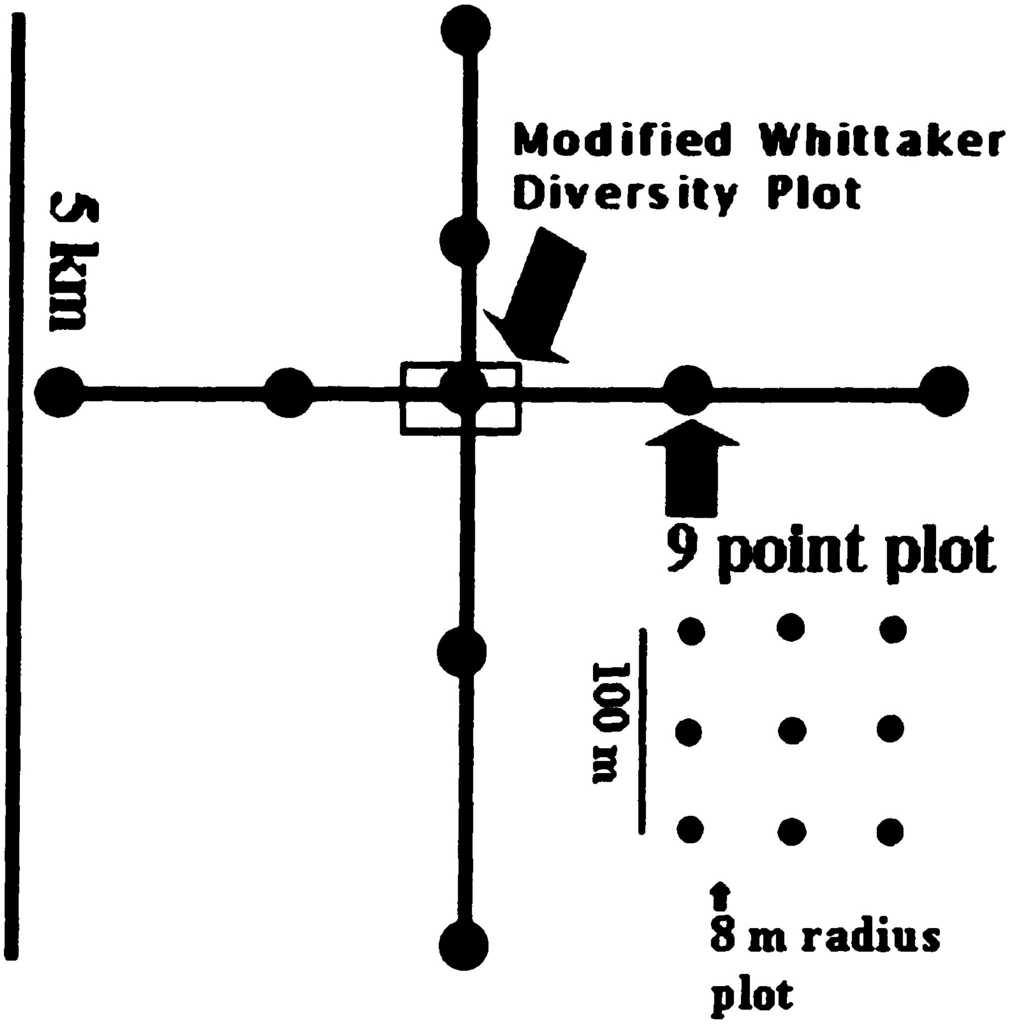

Figure 1-3. The multi-scaled sampling design incorporates two different sampling schemes. Two perpendicular transects were established over a 5 km x 5 km area. Along the two transects, nine plots were laid out at approximately 1 km intervals. At each plot, nine 8-m radius subplots were established. At each subplot, data was collected on grass, forb, shrub and bare ground cover. One modified-Whittaker plot, used to measure vegetation diversity, was located at the intersection of the perpendicular transect.

1.3.4 Spatial Autoregressive Models

The relationship between vegetation structure, diversity and seasonality of grazing was evaluated using the linear relationship:

$$Y_i = \beta_0 + \beta_1 X_{1i} + \cdots + \beta_k X_{ki} + \varepsilon_i \qquad [1]$$

where β_i are regression coefficients associated with the ith independent variable X_i, and ε_i are independent $N(0,\sigma^2)$ random errors, $i = 1,2, \ldots,n$. The models were fitted using ordinary least squares (OLS). Error sums of squares for each model were calculated and tested by the usual general linear test statistic (F-test). A large test statistic supports the alternative hypothesis, Ha, that the inclusion of the independent variables on the right hand side of the equation helps to explain the variability associated with the dependent variables on the left hand side of the fitted regression model.

The residuals from the regression models were tested for spatial autocorrelation using a variation of Moran's I statistic, denoted I_k. If the residuals exhibit a significant spatial autocorrelation, the regression model is refitted using a spatial autoregressive model. If the residuals from the regression model are spatially correlated, this violates the conditions of the OLS model. If the structure of the spatial autocorrelation is known, generalized least squares can be used in the modeling process. Expressing the regression relationship in matrix notation

$$Y = Xb + e$$

where Y is an n x 1 vector of the dependent variable, X is a n x $(k+1)$ matrix of independent variables, b is an $(k+1)$ vector of regression coefficients, and e is an n x 1 vector of residuals, which we assume to be spatial correlated. If we assume the errors in regressing Y on X follows a spatial AR model, then the regression relationship can be written as

$$\begin{aligned} Y &= Xb + (I - \lambda W)^{-1} e \\ Y - Xb &= (I - \lambda W)^{-1} e \end{aligned}.$$

If the errors are normally distributed with mean zero and variance $\sigma^2 D$, then $D^{-1} = (I - \lambda W')(I - \lambda W) = A' A$ and the covariance matrix, V, is given by

$V = \sigma^2 (I - \lambda W)^{-1} ((I - \lambda W)')^{-1} = \sigma^2 A^{-1} A'^{-1}$

In these equations, W is an n x n proximity matrix indicating the spatial arrangements of the sample points with respect to one another. The spatial weights matrix is scaled so that all the rows sum to one.

The log-likelihood function for the spatial AR model is given by

$$\log(L) = -\frac{n}{2}\log(2\pi) - \frac{n}{2}\log(\sigma^2) - \frac{1}{2\sigma^2}(e' A' Ae) + \log|A|$$

Assuming λ is known, the maximum likelihood estimators of b and σ^2 are obtained by setting to zero the partial derivatives of $\log(L)$ with respect to b and σ^2. This results in the following estimation equations:

$\hat{b} = (X'A'AX)^{-1}X'A'AY$ which is the GLS estimate of b, .and

$$\hat{\sigma}^2 = \frac{1}{n}\left(Y'A'AY - 2b'X'A'AY + b'X'A'AXb\right)$$

Since the log-likelihood estimates involve λ as part of the definition of the matrix A, we need to simultaneously maximize log (L) with respect to λ as well as with respect to b and σ^2. Substituting the log-likelihood estimates of b and σ^2 this yields the reduced log-likelihood function

$$\log(L) = -\frac{n}{2}\log(2\pi) - \frac{n}{2}\log\left(\hat{\sigma}^2\right) + \log\left|I - \lambda W\right| - \frac{n}{2}$$

The reduced log-likelihood function is then maximized to find $\hat{\lambda}$ for a given $\hat{\sigma}^2$ and $\hat{b}$.

1.4 Results

Diversities (H' diversity, evenness and species richness) in the area that was grazed during the wet season only (SNP) and in the area that was grazed in both the wet season and dry season (NCA) were not significantly different at the 1-m^2 or the 1000-m^2 scale (Table 1-1). No differences in diversity were correlated to density of grazers in either the wet season or the dry season.

The within landscape analysis of diversity was assessed using Jaccard's coefficient. The average overlap of species among plots within the SNP was 24% versus the overlap of species in the NCA was 13%. On average, more unique species were found in plots located in SNP than in the NCA, indicating patchiness of species distributions in SNP.

The combined species list from the two areas (Appendix I) determined that the overlap in species between the two areas was 44% which is larger than the average overlap among plots within areas. Forty-four and 26 unique species were found in the wet season grazed area versus the wet and dry season grazed area, respectively (Table 1-2). The high degree of overlap between areas indicates that the two areas each harbor some unique biota, but share many of the same species.

Dry season grazing pressure predicted by SAVANNA output averaged 3.4 TLU km^{-2} in SNP versus 46.7 TLU km^{-2} in NCA. In SNP it ranged from 3.4 to 5.3 TLU's km^{-2} while in NCA it ranged from a low of 19.7 to a high of 68.7 TLU's km^{-2}. Wet season densities were 40.9 TLU km^{-2} for SNP and 53.83 TLU km^{-2} for NCA (Table 1-3). In the SNP, the range in animal density was from 28.3 to 59.9 TLU's km^{-2} and in the NCA the range was from 37.0 to 108.3 TLU's km^{-2} in the wet season. Using three years of model output, the spatial distribution of animals was variable within both the wet season and the dry season. During the wet season, when the entire short-grass plains are used exclusively by the wildebeest and no livestock are

Table 1-1. Means and standard deviations of H' diversity, evenness, and species richness (1 m^2 and 1000 m^2) are listed of modified Whittaker plots sampled the two different land use areas, Serengeti National Park and Ngorongoro Conservation Area.

[illegible]	[illegible]	[illegible]
H' Diversity	Mean (SD)	Mean (SD)
Diversity	4.37 (1.09)	3.12 (1.33)
Evenness	1.24 (.196)	0.907 (.304)
Species Richness		
1000 m^2	34.2 (11.07)	29.71(11.38)
1m^2	10.54 (1.49)	8.34 (3.20)

Table 1-2. Jaccard's Coefficient results for overlap, and number of unique species between sites location and between the two regions (SNP and NCA).

Jaccard's Coefficient	**SNP**	**NCA**
Between Sites		
Mean Overlap Between Sites	24. 4% ± 0.18%	13.1% ± 8%
Number of Unique Species	16.8 ± 5.87	11.2 ± 4.60
Between Regions		
Overlap Between Regions	44%	
Number of Unique Species	44	26
Total Species	100	82

Table 1-3. Average SAVANNA generated tropical livestock units (animal densities) for SNP and NCA during the wet season and the dry season.

Season of Grazing		**Tropical Livestock Units**	
		SNP km^{-2}	**NCA km^{-2}**
Wet	Min	28.3	38
	Max	59.9	108.3
	Mean	40.9	53.8
Dry	Min	3.5	19.7
	Max	5.2	68.7
	Mean	4.5	46.8

present, animal densities were still higher in NCA than SNP although these differences in densities were not significant. During the dry season, animal densities were significantly greater in NCA versus the adjacent SNP. This is entirely due to the presence of the Maasai livestock using this area after the migrating wildebeest have moved on. This is a change in the grazing regime compared to the pre-livestock era.

The relative abundance of forbs and shrubs was greater with increasing dry season animal density (p-value = 0.03, 0.02, respectively) and shrub relative abundance was negatively correlated with wet season grazer density (p-value = 0.04; Table 1-4). The relative abundance of grass was negatively correlated (p-value = 0.02) with dry season grazer density and independent of wet season grazer density. Grass cover was independent of wet season grazer density but negatively correlated (p-value < 0.001) with dry season grazer density. Shrub cover was negatively correlated with wet season grazer density and positively correlated with dry season grazer density (p-value < 0.001). Forb cover was independent of both wet and dry season grazing pressure. Bare ground was independent of wet season grazer densities and was positively correlated with dry season grazer density (p-value = 0.01). Grass height was positively correlated with wet season grazer density (p-value = 0.04) and independent of dry season grazer density. Shrub height was negatively correlated with wet season grazer density and positively correlated with dry season grazer density (p-value = 0.002). Forb height was independent of grazer density in both seasons.

Table 1-4. Correlations between animal densities during the dry season and the wet season with relative abundance and cover of grass, forbs, shrubs and bare ground, p-value < 0.05, NS = not significant.

		Dry Season	**Wet Season**
Relative abundance:			
	Grass	-	NS
	Forbs	+	NS
	Shrub	+	-
Cover			
	Grass	-	NS
	Forb	NS	NS
	Shrub	+	-
	Bare ground	+	NS
Height			
	Grass	NS	+
	Forb	NS	NS
	Shrub	+	-

1.5 Discussion

The analysis did not detect any significant differences in diversity between the two areas at any of the scales examined, and differences in diversity were not correlated with animal densities at different times of the year. This result is consistent with predictions made regarding the influence that grazing can have on diversity in semi-arid ecosystems with long evolutionary histories of grazing (Milchunas et al. 1988, Stohlgren et al. 1999). Decreases in diversity in the Serengeti were detected with the removal of grazing (McNaughton 1985), but it is not surprising that no difference in diversity was detected with increases in animal densities or changes in the timing of grazing.

Within the wet season, spatial variations in vegetation composition and structure were correlated with animal density distributions. Areas with higher densities of animals had a higher relative abundance of grass and increased grass cover. Indeed the SAVANNA model was parameterized so that animals responded to increased forage availability so they would concentrate in areas of higher grass cover and productivity during the wet season. However, the correlation here was between the predicted distribution from SAVANNA, and actual field data for plant abundances. During the wet season when water is readily available, animals move in response to localized green-ups (McNaughton 1985) and are more spatially distributed over the landscape. During the dry season, close proximity to water is an important constraint on animal distributions (Illius and O'Connor 1999). Forage during the dry season is of substantially lower quality overall than is available during the wet season, and the benefits of seeking scarce, higher quality forage during the dry season are likely outweighed by the necessity of being in close proximity to water (Pickup et al. 1998, Weber et al. 1998). The grazing range during the dry season is reduced by this constraint and as a result areas near water points are not only grazed throughout the year, but also experience higher average animal densities.

Increases in dry season grazer densities were correlated with increases in relative abundances of forbs, shrubs, and bare ground. On the Serengeti short-grass plains, short stature grasses are predominant, and the relative abundance of forbs is small compared to grasses (McNaughton 1983, Belsky 1995). Short stature and other graminoid traits may have evolved over thousands of years in response to heavy grazing during the wet season. These traits may provide a competitive advantage of graminoids relative to the establishment of forbs.

Much of the short-grass plains is dominated by graminoids with shallow, dense, finely structured roots that efficiently capture rainfall, enabling them to reestablish growth within three days of the first initial rainfall event (McNaughton 1985). This capitalization on water resources early in the growing season allows the grasses to out-compete the forbs early in the growing season. Removal of senescent aboveground shoot material in the dry season should have little effect on grass growth, so it is puzzling why grass abundance might be negatively affected by dry season grazing. One possible mechanism would be that heavy grazing reduces aboveground biomass which could in turn decrease rainfall interception and increase infiltration and bare soil evaporation (Klaismeier 1999, Aguiar and Sala 1999). Increased water inputs to the soil would then cause water to infiltrate to deeper depths, thus reducing the competitive advantage afforded by the fine dense root structure of the grasses. Water may also reach deeper depths where shrubs are rooting. Another possibility is that changes in aboveground litter inputs cause changes in the belowground flora and fauna, which have been shown to affect plant growth (Hooper et al. 2000).

Changes in relative abundances of plant functional groups have been shown in other grazing ecosystems where the temporal component of the grazing regime has changed (Eckert and Spencer 1987, Detling and Whicker 1988, Bork et al. 1998). Indirect effects, which are often extremely difficult to demonstrate, are hypothesized to be responsible for changes in plant functional group abundance. In particular that the mechanism is an increase in bare ground cover, which leads to increased evaporation, reduces soil water, and an overall reduction in biomass and production. Grasses in this ecosystem are thought to have evolved to withstand heavy grazing and out-compete forbs when grazed during the wet season. But, when grazing also occurs during the dry season, indirect effects mediated by ecosystem processes seem to increase the competitive abilities of forbs and shrubs relative to grasses.

Changes in species distribution, composition and structure have possible implications for wildlife, due to reduced forage biomass and higher relative abundances of unpalatable species. Results from this study indicate that some of these changes are correlated to increased grazing during the dry season. This system has evolved under heavy grazing, yet the grazing regime historically has been limited to the wet season only. Changes in vegetation structure and composition were found between areas that are now grazed during both the dry season and the wet season and those that are only grazed during the wet season.

This was a comparison study of vegetation diversity and structure in two areas having different grazer densities, spatially and temporally. Comparison studies have limitations. Although vegetation structural differences were correlated to differing densities of animals at different seasons of grazing it is impossible to identify cause and effect using a comparative approach. Because of this limitation, hypothesis can only be made that a change in seasonality of grazing has been the cause of changes in vegetation structure. Semi-arid systems with long evolutionary histories of grazing have been shown to be extremely resilient to grazing and removal of grazing would probably be a much larger disturbance than increased stocking rates or switches in the time of year the system is grazed (McNaughton 1985, Ellis and Swift 1988, Milchunas et al. 1988). Results from this comparison indicate that increases in dry season grazing may be bringing about changes in vegetation composition and structure yet an experimental approach would be needed to determine cause and effect.

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CHAPTER II: RELATIONSHIPS AMONG SPECIES RICHNESS, PRODUCTIVITY AND SCALE ALONG A PRECIPITATION AND NUTRIENT AVAILABILITY GRADIENT IN SERENGETI, EAST AFRICA

2.0 Abstract

In the Serengeti ecosystem, Tanzania, East Africa, the edaphic properties of the soils produce a nutrient availability gradient that runs counter to a water availability and productivity gradient. Using multiple plot sizes, species richness was examined along this gradient to: 1) relate species richness to patterns of water availability, productivity, and nutrient availability at multiple spatial scales; and 2) determine if these relationships are scale-dependent. Species richness in subplots (1 m^2) was independent of water availability, production and nutrient availability, while plot (1000 m^2) species richness had a positive linear, not unimodal, relationship with an environmental gradient of increasing water availability and primary production and decreasing nutrient availability.

In addition, species richness at the subplot scale was positively correlated to species richness at the plot scale and at each larger scale the relationship became stronger. The slope of the species-area curve calculated for each plot increased with increasing water availability and production. At higher water availability and higher production, species richness accumulated at a faster rate with area. This suggests that the relationship between species richness and abiotic and ecosystem variables is scale dependent and theories that apply to one scale do not necessarily apply to others.

2.1 Introduction

Ecologists have yet to develop a unifying theory that explains patterns of vegetation species richness (Palmer 1994). Careful examination of empirical data has led to many theories about different processes acting on species richness (Grime 1973, Grime 1979, Huston 1982, Tilman 1982, Grace 1999). It has also been acknowledged that different processes act at different spatial scales (Shmida and Wilson 1985, Wright et al. 1993, Weiher 1999, Crawley and Harral 2001). Yet, most studies examine species richness patterns based on plots that are $1 m^2$ or smaller (Kareiva and Anderson 1988, Stohlgren et al. 1997), and it has even been suggested that large plots provide little added value in predicting patterns of species richness (Bond 1983). If different processes are acting at different scales, and ecologists, are consistently sampling at small scales, it is possible that important processes acting at larger scales are being missed and ultimately excluded from theoretical consideration (Kareiva and Anderson 1988, Stohlgren et al. 1997).

The objective of this study was to determine at what scale and to what extent ecosystem variables can be used to explain patterns of species richness across an environmental gradient. Environmental gradients provide a natural framework for examining the influence of processes on ecological patterns. In the Serengeti Ecosystem, Tanzania, there is a pronounced water availability gradient. At the low end of the water availability gradient, the soils are eutrophic and as precipitation increases along the gradient, soils gradually transitions to nutrient poor dystrophic soils (Bell 1983, Frank and McNaughton 1998). The nature of the parent material creates a nutrient availability gradient which runs counter to the precipitation gradient (Ruess and Seagle 1994). The dry end of the water availability gradient is heavily grazed and grazing intensity decreases with increasing water availability (Wilmshurst et al. 1999, McNaughton 1984, McNaughton 1985). Patterns of species richness were investigated using multiple scaled species richness sampling, at subplot (1 m^2), plot (1000 m^2), and landscape scales along the gradient of water availability, nutrient availability, and primary productivity.

The Serengeti is an ideal system to study species richness patterns not only because of the pronounced environmental gradients but also because very important earlier work was done on this system (McNaughton 1983). Biodiversity studies concentrating on grasses by McNaughton found that community composition could be made using precipitation zones. Spatial heterogeneity was important in defining larger area patterns of diversity, (beta and gamma diversity) and small scale diversity was best explained by pattern diversity. While McNaughton concentrated primarily on grasses for his extensive analysis of community composition and diversity, this work is focusing more on the relationships between the patterns of the entire herbaceous community as they are directly related to the gradient while also examining the issue of scale.

A prevalent hypothesis is that species richness should increase as environmental stress lessens (Austin and Austin 1980, Campbell and Grime 1982, Grime et al. 1987, Keddy 1992, Weiher and Keddy 1995). Water is a limiting resource in the Serengeti ecosystem (McNaughton 1983, Bell 1982, deWit 1978) and some theories of species richness focus on the most limiting environmental resource as the primary determinant of richness patterns (Grime 1973, 1979). Secondly, it has been hypothesized that species richness patterns at larger scales are influenced by larger scale processes such environmental filters acting on the species pool (Box 1981, Shmida and Wilson 1985, Keddy 1992, Weiher and Keddy 1995, Stohlgren et al. 1999, Grace 1999, Crawley and

Harral 2001) and that these larger scale processes are directly influenced by environmental factors such as water and nutrient availability (Grime 1979, Zobel et al. 1994, Zobel 1997, Gough and Grace 1998, Grace 2001). At small scales, while large scale processes can influence small scale patterns, their influence is thought to be less direct i.e. though competition for resources among and between species (Gough et al. 1994, Grace 1999, Gross et al 2000) indicating that these different processes might determine plant diversity at different spatial scales (Crawley and Harral 2001).

The third objective of this study was to determine if species richness patterns are similar at the different scales sampled. The 'species pool' hypothesis (Taylor et al 1990, Zobel 1992, Eriksson 1993) suggests that patterns of species richness are caused by the size of the available species pool and this pool is invariant with scale. Richness at large scales would be correlated to other scales (Partel et al. 1996, Wisheu and Keddy 1996). Yet, studies in wetland habitats have demonstrated that this need not always be the case (Weiher 1999). If species richness is directly scaleable (i.e. processes acting at one scale act at all scales) then high correlations would be expected of species richness between all scales measured making it possible to predict species richness at larger scales by sampling at the smaller scales. Conversely, if different processes are acting at the different scales, then small-scale species richness should not be correlated or weakly correlated to large-scale species richness making it difficult to estimate large scale richness from small scale samples. To develop a comprehensive theory on species richness, it is important not only to understand at what scale different processes are acting at but also if relationships exist between different scales of measurement. If relationships between the different scales do exist, then ultimately determining what connects those relationships will provide ecologists with a better understanding of diversity patterns across scales.

2.2 Methods

2.2.1 Study gradient

The Serengeti ecosystem is situated east of Lake Victoria and northwest of the Ngorongoro highlands and the Rift Valley and covers approximately 27,000 km^2. This ecosystem is one of the most heavily grazed systems on earth (McNaughton 1985) and is functionally defined by the seasonal migration of over 1.5 million wildebeest (Pennycuick 1975, Sinclair and Norton-Griffiths 1979) (Figure 2-1). The wildebeest travel to the short-grass plains during the wet season where they graze on the short stature (~ 5-10 cm) nutritious grasses during the short growing season. The migration is very concentrated on the short grass plains during the wet season and wildebeest graze intensively until the grass begins to senesce. After the grasses senesce, the wildebeest travel north through the midgrass plains, which is generally a transition area for the migration and is not as heavily grazed as the short-grass plains. Grasses in this transition zone can grow up to 1 m tall. The change in stature of the grasses is accompanied by a switch in species composition. At the high precipitation zones in the north where the growing season in the longest, the tall grasses grow up to 2 meters. This change in stature is also associated with switches in species composition.

Soils in the southern portion of the park are eutrophic, derived primarily from volcanic material, alkaline, clayey and rich in organic carbon and nutrient stores (deWit 1978). In higher rainfall zones, soils are dystrophic, granite derived, highly weathered, heavily leached, with moderate to extreme acidity (Jager 1974). These types of soils contain low to moderate levels of organic carbon, nitrogen, phosphorus and micro-nutrients (Frank and McNaughton 1998).

Primary production in areas with dystrophic soils is more limited by nutrients than by precipitation, and plants typically produce aboveground tissues with higher C:N ratios and lignin concentrations (Bremen and deWit 1983).

2.3.2 Sampling Design

Species richness was measured using a modified-Whittaker plot design (Stohlgren 1995). The modified-Whittaker design is multi-scaled, covering a total area of 1000 m^2. Nested within the 1000-m^2 plot are ten 0.5 x 2 m (1-m^2) subplots, two 2 x 5 m (10-m^2) subplots at opposite corners, and one 5 x 20 m (100-m^2) subplot at the plot center. Percent cover and height by species were recorded in the 1-m^2 subplots. At the other scales within the plot, species presence was recorded. Subplot (1 m^2) species richness was calculated by averaging the richness numbers from the ten 1-m^2 subplots, and plot (1000 m^2) richness was calculated as the sum of all species found in the 1000-m^2 plot. Fifty-eight modified-Whittaker plots were established across the gradient.

2.3.3 Ecosystem data

Water availability was defined as the ratio of precipitation to potential evapotranspiration. A low precipitation:PET ratio indicates low moisture relative to high incoming solar radiation and thus increasing soil moisture stress for vegetation. Precipitation data were collected for over 40 years at over fifty rain-gauge locations throughout the

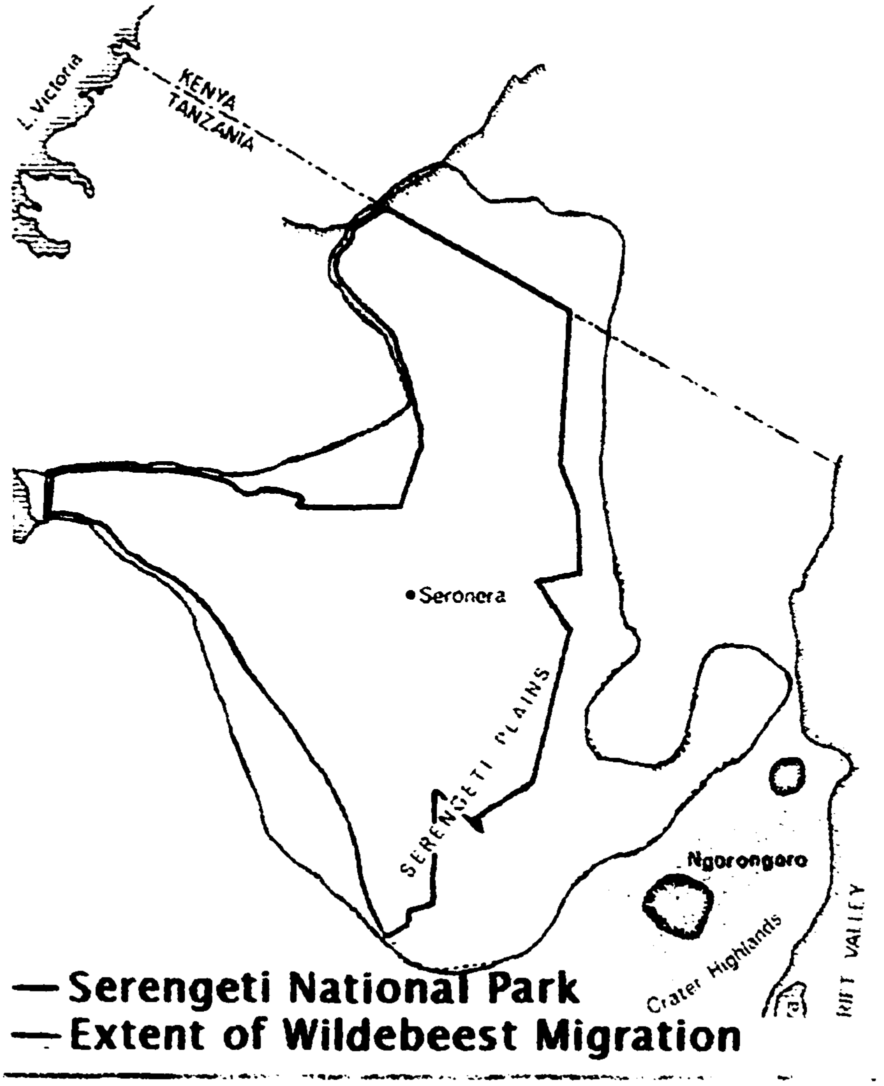


Figure 2-1. The Serengeti ecosystem and area of wildebeest migration.

ecosystem. Yearly precipitation values were interpolated using inverse distance weighing based on four nearest neighbor sample points to create grid coverages of mean annual precipitation. Potential evapotranspiration (PET) was calculated using the Priestly-Taylor method which uses solar radiation and temperature. A map of water availability (Figure 2-2) was derived by dividing the precipitation map by the PET map.

Annual net primary production was estimated using 10-day composites of daily Normalized Difference Vegetation Index (NDVI) data (Prince 1991, Rasmussen 1998) which was averaged over three years (EROS Data Center, USGS, Sioux Falls, SD). The integrated NDVI data were calibrated to field productivity data (McNaughton 1983) that was sampled for grasslands throughout the ecosystem using linear regression. The primary production field data did not take into account the woody vegetation, which is perhaps one of the reasons for the low explanatory ability of the regression model ($R^2 = 0.25$). The regression model was then applied to the NDVI data to produce the map in Figure 2-3. Annual net primary production is defined as: iNDVI * 93.28 -1641.1 ($n = 32$, $R^2 = 0.25$, p-value = 0.004) and calibrated to field production measurements.

Nutrient availability was analyzed by considering total pool sizes of carbon, nitrogen and phosphorus and the turnover indices of nitrogen mineralization, soil respiration or microbial biomass. Thus, large total pools and high turnover rates both promoted nutrient availability.

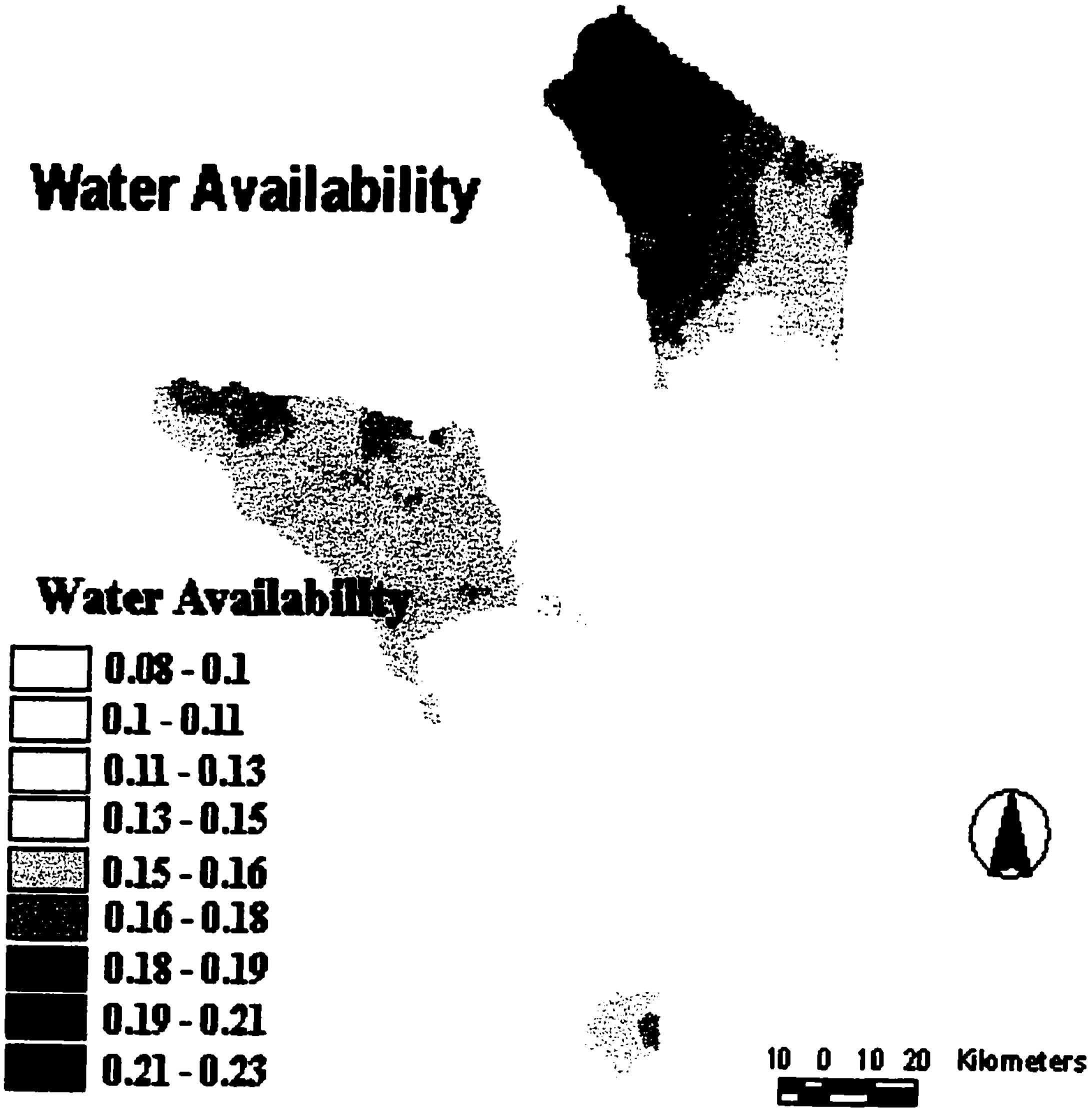


Figure 2-2. Water availability measured as the ratio of precipitation to potential evapotranspiration over the Serengeti.

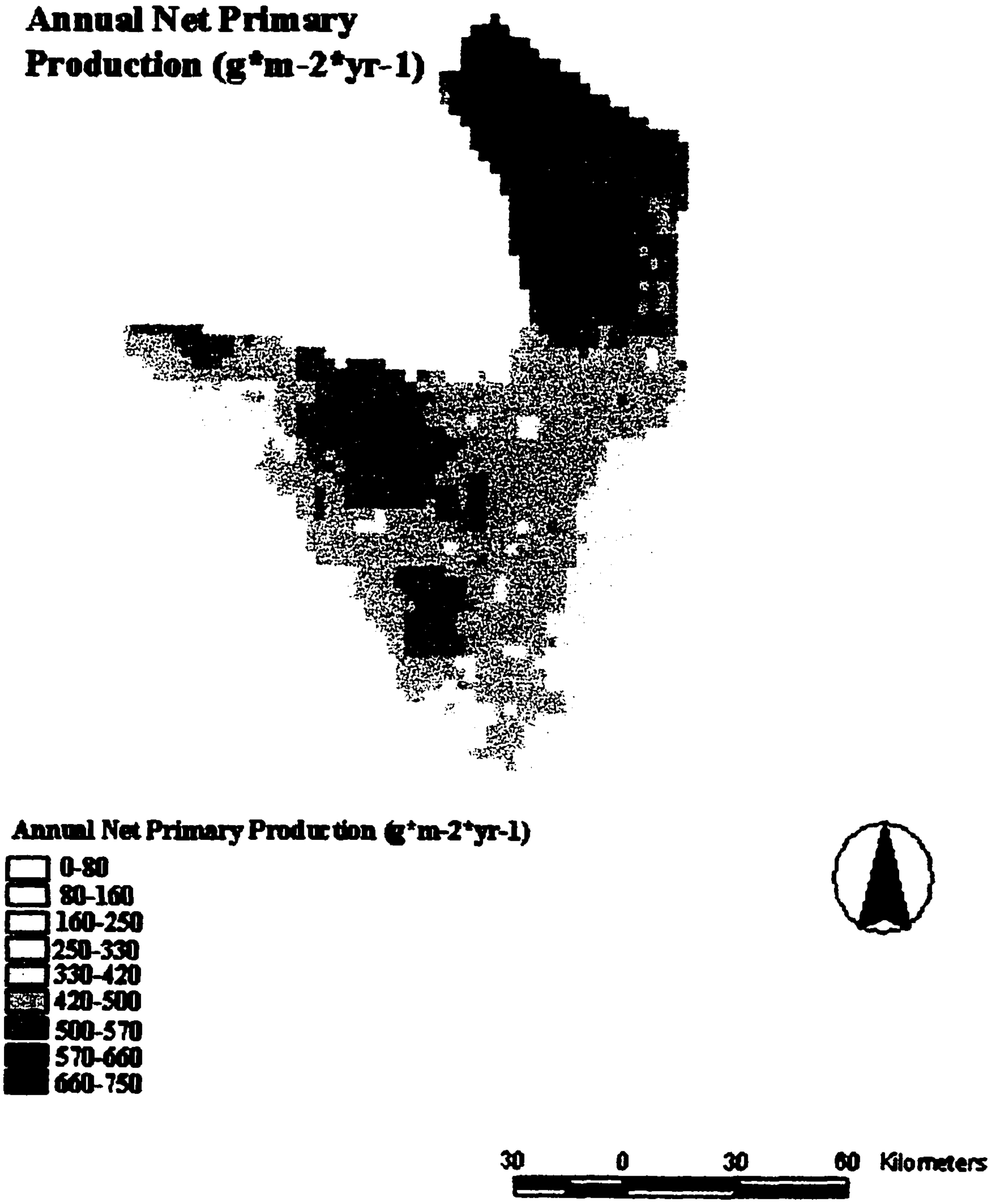


Figure 2-3. Map of estimated primary production, using integrated NDVI data calibrated.

Total nutrient pool data (Ruess and Seagle 1994) were spatially interpolated to create a regional map. Potential (maximum) nitrogen mineralization and soil respiration rates were converted to water and temperature-limited rates by using a decomposition factor (Parton et al 1987). The decomposition factor takes into account variations in elevation, temperature and solar radiation across the landscape using a combined function of temperature, PET, and precipitation as used to affect decomposition rate in the CENTURY model (Parton et al. 1987). Microbial biomass data from Ruess and Seagle (1994) were spatially interpolated over the landscape.

2.3.4 Data Analysis

Data were analyzed using backwards step-wise multiple regression and path analysis (criteria p-value < 0.05). Variables in the model included total pools of carbon, nitrogen, and phosphorus, nitrogen mineralization and soil respiration rates, microbial biomass, cation exchange capacity, soil pH, NDVI derived net primary production and water availability. The multi-scaled species richness data within plots were fit to log species-area curves and slopes of the species area curve for each modified-Whittaker plot was plotted against water availability and primary production. Landscape scale species richness was determined by randomly selecting five modified-Whittaker plots from each precipitation zone and treating the summation of the species list for the five plots as an estimate of the available species pool. Randomized species accumulations curves were created for each precipitation zone (Colwell, 2000).

2.3 Results

Estimated primary production was positively correlated with water availability measured as the ratio of precipitation to potential evapotranspiration (Figure 2-4). Species richness at the plot (1000 m^2) scale was positively correlated with primary production ($r = 0.48$, p-value < 0.001) and water availability ($r = 0.58$, p-value < 0.001) and relationships between water availability and production became weaker with decreasing scale (Figure 2-5). No significant correlations were found at the subplot scale (1 m^2) or at the 10 m^2 scale. At low water availability, production and species richness at the plot scale (1000 m^2) was lowest. Highest levels of water availability occurred at the highest productivity values and the highest species richness occurred at the plot (1000 m^2) scale.

Species richness was negatively correlated to nutrient availability. Total pools of carbon, nitrogen and phosphorus were negatively related to species richness at the plot and regional scales and were either weakly negatively correlated with or independent of turnover indices (Table 2-1).

Multiple regression analysis determined that soil nitrogen was the only statistically significant variable predicting plot level species richness. Path analysis was then used to determine the relative importance of multiple nutrient availability and primary productivity (Figure 2-6). Nitrogen mineralization per gram of carbon and the soil carbon to nitrogen ratio had positive relationships with plot species richness while aboveground production had a weak negative interaction with species richness.

Subplot (1 m^2) species richness was positively correlated to 1000 m^2 plot species richness (Figure 2-7) and increasing the scale of sampling from 1 m^2 to 100 m^2 explained more of the variance in species richness at 1000 m^2. Subplot species richness explained 33% of the variation in plot species richness while 100 m^2 species richness explained 78% of the variance in species richness (1000 m^2). The slopes of the plot-scale species-area curves showed that the rate of species accumulation within plots increased linearly across the water availability and production gradients and thus decreased along the grazing and nutrient availability gradients. The slopes of the species-areas curves of each plot were positively correlated to both production and water availability (Figure 2-8).

Table 2-1. Relationships between nutrient pools or nutrient turnover indices and species richness at subplot (1 m^2) and plot (1000 m^2) scales, n = 58.

Plot (1 m2) scale		
Total pools	r	p-value
Carbon	-0.29	0.24
Nitrogen	-0.27	0.04
Phosphorus	-0.14	0.2
Turnover indices		
N Min	-0.31	0.03
Soil resp	-0.04	0.46
Microbial Biomass	-0.04	0.45
Water Availability	0.41	0.03
Primary Production	0.14	0.35
Site (1000 m2) scale		
Total pools	r	p-value
Carbon	-0.62	<0.001
Nitrogen	-0.67	<0.001
Phosphorus	-0.61	0.0001
Turnover indices		
N Min	-0.03	0.49
Soil resp	-0.4	0.01
Microbial Biomass	-0.49	0.001
Water Availability	0.57	<0.001
Primary Production	0.5	0.001

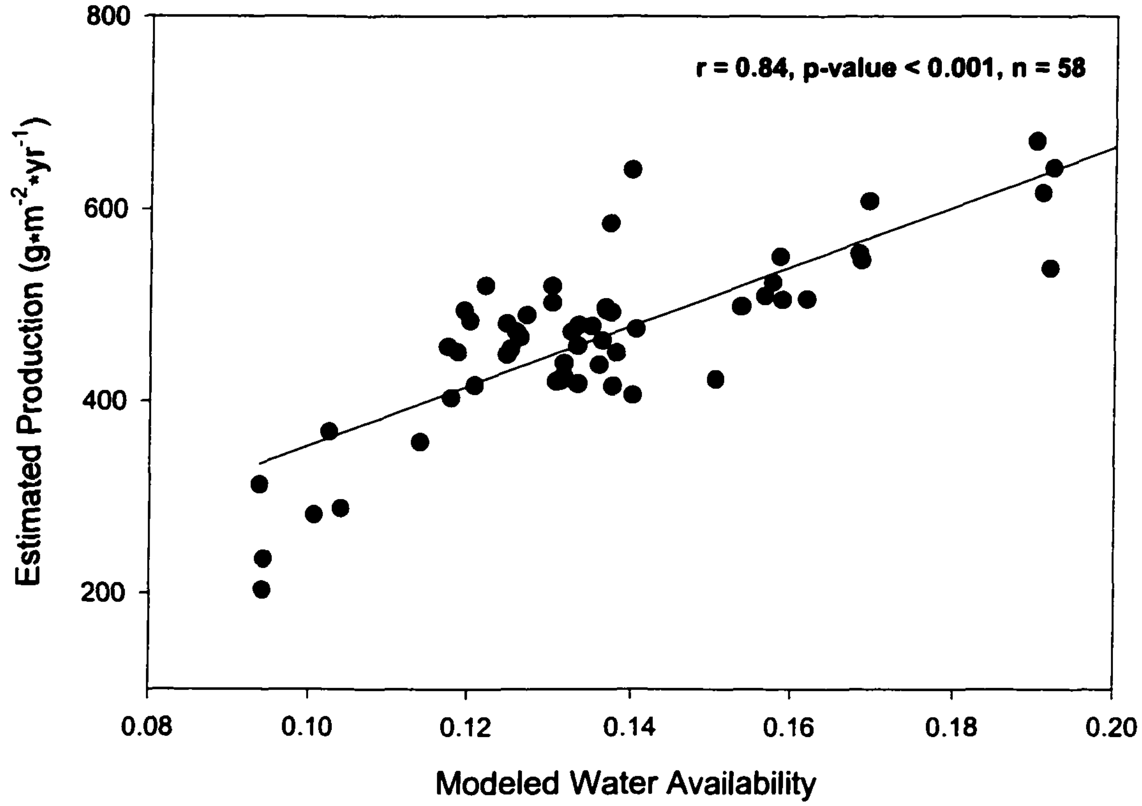


Figure 2-4. Relationship between primary production and water availability measured as the ratio of precipitation to potential evapotranspiration, ($r = 0.84$, $n= 58$, p-value < 0.01).

These results indicate that while the number of species per unit area in a subplot is constant across the area (Figure 2-5), the number of additional species found by adding a given area to the sample increased with water availability and primary production. Landscape patterns of species area curves using combined plots (landscape level richness) showed that in higher precipitation zones, the initial estimate of species at the plot scale increased with increasing precipitation yet the relative slopes increased in a consistent way (Figure 2-9).

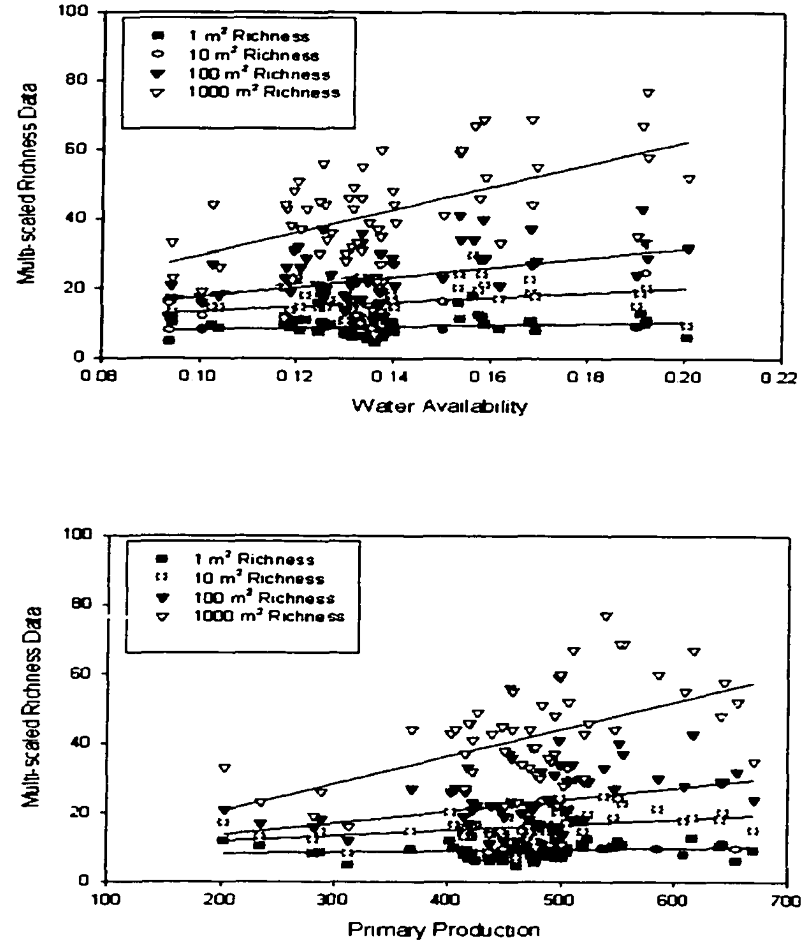


Figure 2-5. Relationships of multi-scale species richness with water availability and primary production. As the size of the plots increases, the relationships became stronger.

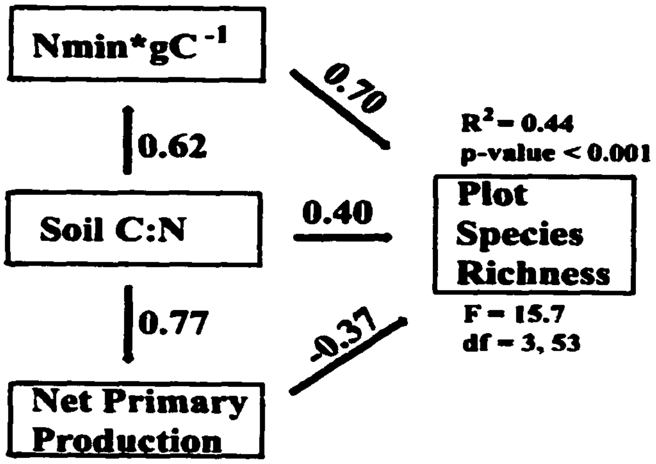


Figure 2-6. Path analysis performed on the nutrient availability and primary productivity data determined that soil substrate (C:N ratio and nitrogen mineralization per gram of carbon) had a positive effect on relationship with species richness at plot scales and primary production had slight negative effect or relationship with richness patterns.

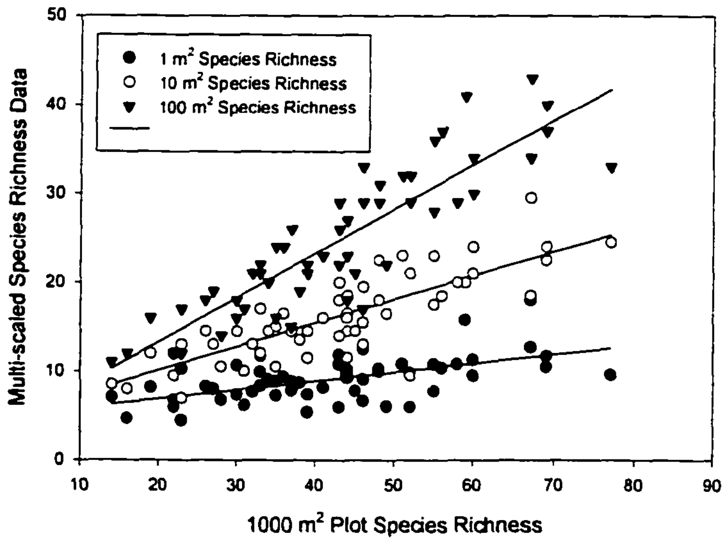
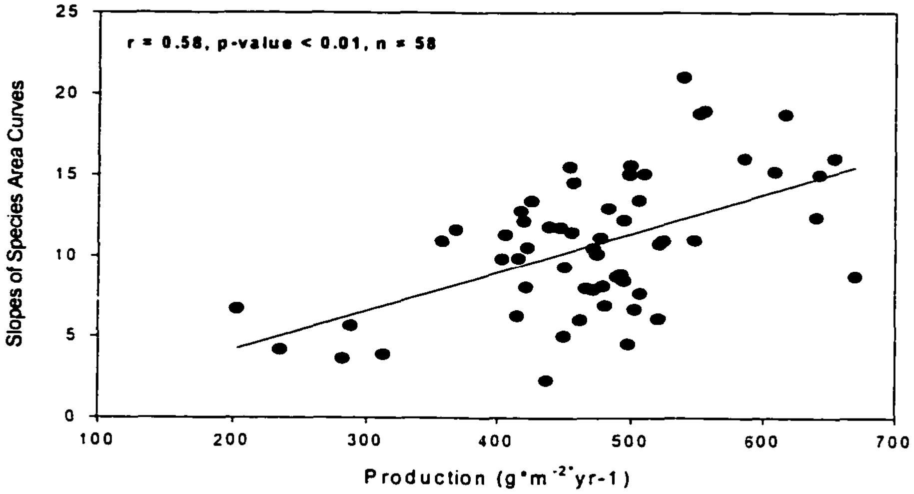


Figure 2-7. Relationships between subplot ($1 m^2$), 10 m^2, 100 m^2, and plot (1000 m^2) species richness, r = 0.61, r = 0.80, r = 0.88, respectively, n= 58, p-values < 0.001.



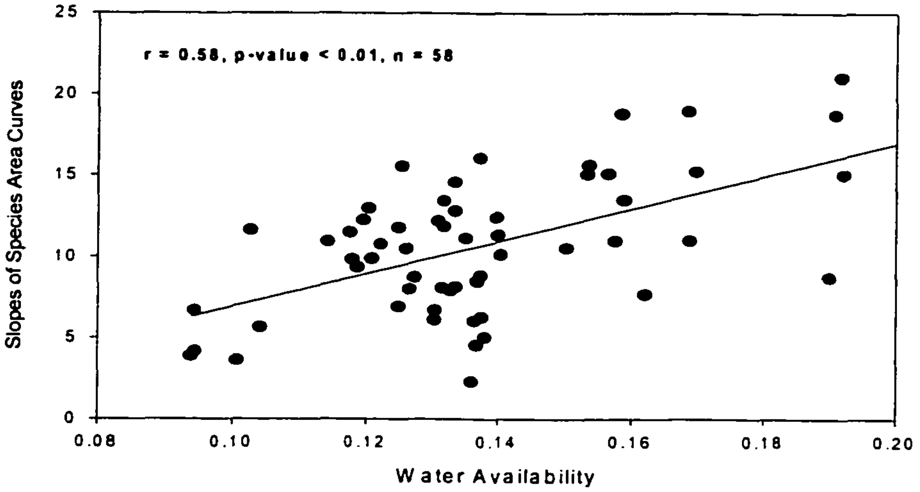


Figure 2-8. Slopes of the species area curves versus primary production ($r = 0.58$, p-value < 0.01, $n=58$) and water availability($r = 0.58$, p-value < 0.01, $n= 58$).

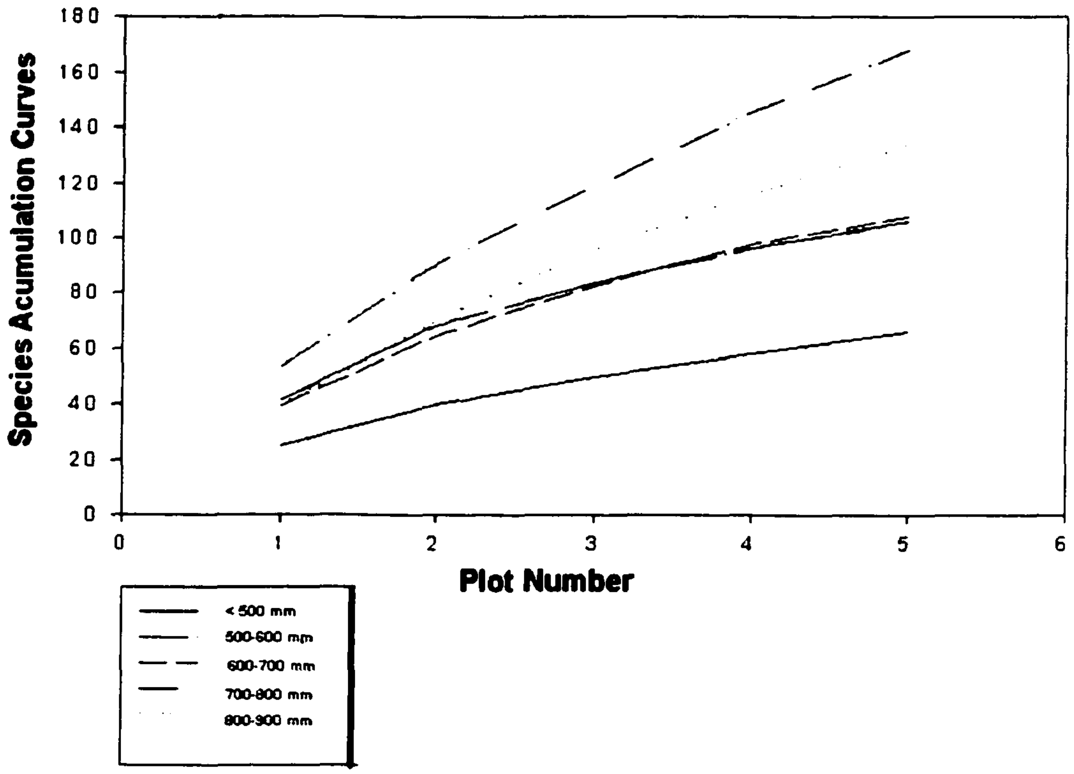


Figure 2-9. Landscape scale species accumulation curves based on five random plots within each precipitation zones. As precipitation increased, the number of species in the first plot increased and species subsequently accumulated at a faster rate with added plots indicating that as precipitation increases, the available species pool increases.

2.4 Discussion

Using the plot scaled data, significant relationships were found between species richness and water availability, production, and nutrient availability. Water availability alone was able to explain 32% of the variance in species richness at the plot scale. One possible explanation for these plot scale patterns is that species traits are convergent in both grazed and water limited environments (Coughenour 1985, Milchunas et al. 1989), potentially limiting available species pools (Box 1981, Keddy 1992, Grace 1999) at the drier end of the rainfall gradient. Manipulation experiments have demonstrated that environmental conditions such as low water availability or high levels of salinity can filter out the number of species which are adapted to that environment (Weiher and Keddy 1995). These filters ultimately reduce the number of species that can colonize and persist in an area. In the Serengeti ecosystem it is proposed that species traits diverge when assemblages are released from environmental and grazing constraints, thus increasing the available species pool, and finally species richness. The theory that traits converge under environmental stress and diverge when released from the limiting constraint would predict not just fewer and more similar species at low water availability but also similarity of morphological traits (Weiher and Keddy 1995). Although morphological traits were not measured, species richness did increase at plot scales with increasing water availability. Along this gradient, locally rare species contributed to higher species richness at sites with higher water availability and production. One possible hypothesis could be that in grazed ecosystems, at locations where conditions are water limited and heavily grazed, such as the short grass plains, there may be high turnover of common species. Locally rare species that contribute disproportionately to the species pool are few compared to sites with high water availability.

The relationship between species richness and productivity is one of the most cited relationships in ecology (Mittelbach et al. 2001). The most common form of this relationship in vegetation diversity studies is the unimodal curve (Grime 1972, 1979, Huston 1979, Tilman 1982, Rosenzweig 1992). Yet, the plot data here demonstrated a linear relationship between richness and productivity. The 'species-energy' theory predicts the pattern that was observed in this system. The premise of the 'species-energy' theory is that richness can be predicted by the amount of energy that is incorporated into a system. This theory has been used successfully to explain patterns of increasing species richness with production over very large (continental) scales (Currie and Paquin 1987, Currie 1991) and could provide a partial explanation for the patterns we observe in this system. Another explanation for the linear increase could be that increased nutrient limitation at the wetter and more productive end of the gradient contributed to more possibilities for species coexistence, as proposed by Tilman (1988). Relationships between the available nutrient pools and the turnover rates showed that as species richness increased, available nutrients declined. Path analysis confirmed this relationship with the substrate quality represented in the soil carbon to nitrogen ratio and the amount of nitrogen that was turned over per unit of carbon (Figure 2-7). While overall nutrient availability declines with increasing precipitation (Table2-1), the amount of nitrogen per unit of carbon is positively correlated to richness. Overall, the flux of nitrogen is negatively correlated to richness patterns. The flux of nitrogen per unit of available carbon was positively correlated, determined by path analysis, confirming the negative relationship between nutrient availability and richness patterns. In the Serengeti, it has been shown that at the high water availability end of the gradient, production increases when nitrogen is amended to the system, indicating that production is more limited by nutrients than by water (S.J. McNaughton pers. comm.). In heavy nitrogen addition experiments, increases in productivity brought about decreases in species richness (Vitousek et al. 1997, Hooper and Vitousek 1997). If this generality were applied to the Serengeti, species richness potentially would decline if productivity was not limited. Path analysis demonstrated a slight negative effect from production on species richness indicating that with continued increase in production, richness would eventually decline. Grazing can also be argued to account for the linear (not unimodal) trend that is observed in this system. In the highly productive tall grass prairie of North America, biomass reduction due to grazing has been correlated to increases in vegetation diversity (Collins et al. 1995). It could be argued that a similar explanation could be used in this system to explain this linear trend in richness (Huston 1972).

Water availability was only able to explain 32 % of the variance in species richness patterns at the plot scale. That leaves a considerable amount of variance in richness that was not explained. Furthermore, no relationships could be found between the environmental and ecosystem data and subplot richness. Indeed, it is likely that had small scale variables such as competitive interaction been sampled, relations between species richness and the variables most likely would have emerged and potentially reduced some of the unexplained variance. Processes acting at small scales do not necessarily scale-up to larger scales, thus is may be difficult or impossible to use a single explanation for species richness at all scales (Bond 1983, Palmer 1994, Stohlgren et al. 1999).

Positive relationships were found between species richness and the different scales measured. Subplot-scale species richness was able to explain 33% of the variation of the plot-scale species richness and this percentage increased with increasing sample size. More locally rare, patchily distributed species are captured with successively larger plots, resulting in stronger correlations with the 1000 m^2 plots which captured the greatest number of species. The increasing correlation between richness at the small and larger scales supports the 'species pool hypothesis' which purports that species composition at some critical area size is completely representative of the species pool for larger areas (Grime 1973, 1979, Zobel 1992, Eriksson 1993). Theoretically, it has been suggested that species accumulate at a relatively constant rate with increased area(Connor and McCoy 1979, May et al. 1975, Sugihara 1980) but field studies have demonstrated that species do not necessarily accumulate at constant rates across different habitat types (Daubenmire 1968, Bond 1984, Stohlgren 1997, Crawley and Harral 2001). The slopes of the species area curves demonstrated that species accumulate at different rates across the Serengeti environmental gradient. Species accumulated at faster rates per unit sampled area at the high production end of the gradient. At the landscape level, species accumulation curves showed that the number of species in the first plot selected increased with increasing precipitation and the slopes generally had the same shape indicating that species numbers in the plot is reflective of the total number of species in an area.

The 'species-energy' theory predicts that in higher productivity regions, species accumulate at a faster rate than in low productivity regions (Currie 1991). While the species-energy theory provides a plausible explanation for changes in species richness at regional and continental scales, it is not variation in energy input from the sun that determines patterns in species richness in the Serengeti. Species richness and species accumulation rates increased as environmental constraints were lifted, independent of incoming solar energy. Along this gradient, other environmental constraints limit the amount of solar energy that is fixed by plants, and it is these other constraints which explain species richness patterns.

The number of species that can be packed into a small area is another potentially important constraint on species richness. The number of species that can be packed into a small area is dependent on a number of factors such as the sizes of individual plants and the vertical and horizontal spaces they occupy (Crawley and Harral 2001). In this system, changes in species pool were related to large scale variations in water availability, potential evapotranspiration, and nutrient availability. These factors also influence species morphology. At the low end of this production gradient, species are short statured and more horizontally spreading because of reduced capacities to produce large amounts of aboveground biomass, intense competition for belowground resources and the need to partition resources to structures which escape aboveground herbivory (Coughenour 1985, Milchunas et al. 1989, McNaughton 1994). Increased water availability leads to a change from belowground to aboveground competition for resources (light interception) and species composition shifts to increased prevalence of taller, more erect morphologies. Thus at the subplot scale, a single sample captures a larger proportion of the species pool in low production areas with small vertically spreading plants, compared to the higher production areas with larger, more horizontally spreading plants.

To explain the species richness patterns and scale relationships found in this system, several theories could be used simultaneously and none can be ruled out using an observational study. Theories of species richness work at different scales, therefore a combination of theories is needed to predict species richness patterns. At large geographic scales, much larger than the scales measured here, the species-energy theory predicts many of the patterns that are observed. However, at the scale of this study, variations in the rate of energy fixation and conversion to biomass are driven by different processes than just energy. We propose that water availability and grazing constraints potentially impose filters which limit species pools and influence morphological traits. The morphology of the species influences how many species can be packed into a small area. Production increases with increasing water availability. Because nutrient availability decreases as rainfall increases along this gradient, species richness continues to increase and never reaches a peak at higher production levels as is commonly seen in other studies.

Processes act at different scales, yet a unifying theory that incorporates processes acting at different scales is lacking. Models for species richness can provide an heuristic framework for the integration of different theories by incorporating processes that act at very different scales. Grace (1999) produced a model that is very comprehensive by synthesizing various theories involving processes acting at multiple scales, but predictions were limited to a fixed scale. Results from this study indicate that environmental variables can be successful at predicting large scale patterns but unsuccessful at predicting patterns at smaller scales where generally only common species or habitat generalists are sampled. Most studies in ecology use small plot sizes and as a result, ecological theory may be disproportionately influenced by small scale patterns (Grace 1999). Ideally, theories that can link the large and the small scale processes will be necessary to fully understand and predict species richness patterns across multiple spatial scales.

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CHAPTER III: TREE-GRASS INTERACTION AND SPECIES COMPOSITION ALONG A PRECIPTIATION GRADIENT IN THE SERENGETI NATIONAL PARK, TANZANIA

3.0 Abstract

Savannas are structurally a combination of grasslands and forests. Interactions between grasses and trees have been described as either facilitative or competitive depending on the interacting factors of precipitation, tree size and density. The Serengeti ecosystem spans a number of different ecotones ranging from a true "grassland" that occurs in the low precipitation zone to broad leaf 'tree savannas" at higher rainfall areas. The objective of this study was to describe general trends of vegetation structure of woody canopy cover, size class distribution, and tree density with relation to herbaceous vegetation cover along this precipitation gradient. Species composition along the precipitation gradient is also discussed.

Precipitation was positively related to tree density of all size classes ($r = 0.67$, p-value < 0.05), but relationships were stronger with increasing tree height ($r = 0.47$ trees $<$ 1 m tall, $r = 0.46$, trees 1-3 m tall, $r = 0.66$, trees $>$ 3 m tall). Path analysis, which is an

extension of multiple regression models, revealed that the density of trees in different height classes were not equally important and densities of taller trees were strongly correlated with decreases in herbaceous vegetation cover. Both canopy cover and precipitation had negative correlations with herbaceous vegetation cover, while potential evapotranspiration had a positive interaction. Results from this study indicate that precipitation and the density of trees > 1 m tall, or the size of the trees were correlated more strongly with herbaceous vegetation cover.

Canonical correspondence analysis was performed to relate major environmental characteristics (soil variables, precipitation, slope, elevation and potential evapotranspiration) with species and families of trees. The families and species compositions were characterized by gradients in precipitation, potential evapotranspiration, elevation and cation exchange capacity. Using all available data, canonical correspondence analysis was only able to explain 12.3 percent of the variation in species composition indicating that important influencing variables were missed from the analysis, such as the influence of herbivory and fire. Yet, when tree species were grouped by 100 mm precipitation zones, some very interesting patterns emerged. Very few trees occurred below 500 mm mean annual precipitation, but above that threshold, tree frequency increased and tree species changed with changes in precipitation. Trees belonging to the family Fabaceae comprised over 60 percent of all trees found in zones below 900 mm precipitation and that proportion increased with decreasing precipitation until it reached the 500 mm precipitation threshold. In areas that receive over 900 mm precipitation, trees were evenly distributed between four families: Combretaceae, Ebenaceae, Euphoriaceae and Fabaceae.

3.1 Introduction

Savannas are typically described as communities or landscapes of co-occurring grasses and trees that are neither pure grasslands nor forests, but consist of a mixture of different plant functional types (Huntley and Walker 1982, Scholes and Walker 1993). Many qualitative models have been proposed to explain the co-occurrence of tree and grass functional types in African savannas (Belsky 1990). These models include precipitation, temperature, and evapotranspiration as the major drivers of grass:tree ratios (Whittacker1975, Walker 1987, Scholes and Walker 1993). More complicated models include the importance of herbivory, especially elephants and fire in models to predict grass and tree distributions (Dublin and Sinclair 1990, Dublin 1991).

The ratio of grass cover to tree cover is a primary determinant of the structure of savannas. Woody plants have been shown to alter the production and composition of grasses in savannas in negative, neutral, and positive ways (Basian and Swetnam1990, Belsky 1990, Archer 1990). One hypothesis that explains the effect of trees on increasing herbaceous vegetation is that of facilitation (Calloway 1995). Empirical evidence has shown that under harsh environmental conditions trees can ameliorate water and radiation stress creating more conducive microclimates for understory vegetation (Belsky and Canhan 1994). These phenomena are explained through decreased water loss provided by tree shade (Pressman 1975, Thurow et al. 1987, Dawson 1993), nutrient enrichment beneath tree canopies (Raswanski and Wickens 1967, Kellman 1979, Vitousek and Walker 1989, Blackmore et al. 1990, Weltzin and Coughenour 1990, Belsky and Amundson 1992), and shading (Parker and Muller 1982). Yet, competition between grasses and trees can become more important at higher rainfall zones where there is less water stress (McClaran and Bartolome 1989, Belsky 1994). As opposed to increased vegetation underneath canopies, which is seen in more arid areas, in higher rainfall zones herbaceous vegetation production is relatively lower under tree canopies than in the open, indicating that trees are competing with understory vegetation.

It has also been shown that tree size can influence vegetation production (Engle et al. 1987, Cameron et al. 1989). When trees are small, it is hypothesized that facilitation may be more important than competition. As tree canopies develop, they more heavily influence the microclimate of the area they occupy through increased shading and deeper and more developed root structure. Studies have shown that the negative effects of trees on herbaceous vegetation do not occur until trees reach larger sizes (Stuart-Hill and Tainton 1989, McPherson, et al. 1991, Fuhlendorf et al. 1997). This interaction is then compounded by tree density. As density of trees increases, herbaceous production typically declines (Archer 1990, 1993, 1995).

Fire and herbivory are major determinants of savanna vegetation structure (Walker 1987, Dublin 1991, Sinclair 1995, Dublin 1995) but they are not the focus of this study. In the Serengeti National Park, Tanzania, seedling survivorship declines sharply with increasing fire frequency (Dublin 1995). The frequency and intensity of fire is dependent on the interactions between herbivore densities and fluctuations in rainfall. Fire frequency and wildebeest numbers have been used in relating to tree ring data to determine relationships between grazing, fire frequency, and tree regeneration events. Fire frequency was predicted to be highest in times when wildebeest numbers were low (Sinclair 1995) and the ratio of wet/dry season precipitation was greatest (Stronach 1989). Fire frequency was high in the 1950's and 1960's and fire frequency was low throughout the 1970's and 1980's (Sinclair 1995). Age class distributions of *Acacia robusta* corresponded to the timing of these events, confirming the importance of fire and herbivory in determining vegetation structure. A prescribed burning program was implemented after 1990 to meet a number of management objectives. The influence that this prescribed burning program may have on vegetation structure and tree regeneration in the park is yet to be determined. Information about how fire frequency might change along the precipitation gradient is unknown but it might be suspected to increase with increasing precipitation and primary production.

This study describes savanna vegetation structure and composition along a precipitation gradient in the Serengeti that ranges from 350 mm to over 1100 mm mean annual precipitation. The objective of this study was to examine changes in woody canopy cover, size class distribution, and density in relation to herbaceous under-story vegetation cover along this precipitation gradient. Distributions of tree families and species are also described.

3.2 Study Area

The prevailing northwest direction of storm movements and the location of the Ngorongoro highlands, southeast of the Serengeti National Park causes a rain shadow with reduced precipitation on the southern Serengeti plains. Precipitation increases in a north-easterly direction reaching a mean annual maximum of ~1100 mm. The strong precipitation gradient occurs on a large continuous stretch of land that is virtually uninterrupted by changes in land use which makes this area an ideal place to examine relationships between rainfall, vegetation cover and tree size distribution and composition. Published reports of the vegetation of the Serengeti ecosystem provide lists of species, general descriptions of structure, maps, and aerial photographs from 1972 and 1991, but no detailed quantifications of vegetation structure, woody tree density, height distribution, or woody species composition have been made along this precipitation gradient.

3.3 Methods

One-hundred and eighty plots were randomly located throughout the Serengeti National Park and adjacent short-grass plains. The primary sampling unit was a 100 m x 100 m area, with nine subplots located within the 100 m x 100 m area on a grid, at 30 m x 30 m spacing. At each subplot, an 8 m radius sample plot was established and information was collected on vegetation structure and composition.

On each 8-m radius plot, under-story vegetation data were collected by recording visual estimates of percent canopy cover of grass, forb, shrub and bare ground. Tree height was divided into three height classes; class I = < 1 m, class II = 1-3 m, and class III

= > 3m. Number of trees in each height class and average canopy diameter of trees/height class were recorded at each subplot. Four densitometer readings taken at right angles from one other were averaged to estimate woody canopy cover.

Precipitation data were collected for 40 years at over fifty rain gauge locations throughout the ecosystem by the Serengeti Ecological Monitoring Program. Yearly precipitation values were interpolated using inverse distance weighing to create a map of mean annual precipitation for the area. Six arbitrary precipitation zones were designated at approximately 100 mm mean annual precipitation intervals and tree frequency data and species composition data were analyzed with respect to these precipitation zones.

Values for vegetation and bare ground cover, tree density and size class distribution averaged from the subplot data were assigned to 34 landscape units. The landscape units were based on topographic and geomorphologic classifications (Epp 1981). An average precipitation value was assigned to each of the landscape classification units, and data were then analyzed regionally. Soils data were extracted from surveys conducted in the Serengeti plains (Dewit 1978) and woodlands (Jager 1984).

3.3 Results

Total herbaceous layer vegetation cover; the sum of grass, forb, and shrub cover, was negatively correlated with precipitation (Figure 3.1a). Figure 3.1b shows that the majority of the vegetation that comprises the herbaceous vegetation cover is grass. Tree density, defined as trees/ha, was positively correlated with precipitation (Table 3.1). Precipitation showed the strongest relationship with tree density in the tallest size class while precipitation showed weaker relationships with trees of size class I and II. Total tree density was negatively correlated with herbaceous vegetation cover. Using the ordinary least squares algorithm, multiple regression and path analysis were used to determine the simultaneous contribution of density of trees of different size classes (Figure 3.2). Density of trees in all three size classes had negative interactions on herbaceous vegetation cover, but disproportionately so. Density of trees > 1 m tall had strong negative interaction (standardized coefficient = -0.352 and -0.354, respectively) on herbaceous vegetation cover compared to smaller trees (standardized coefficient = -0.021). Path analysis was then used with precipitation, evapotranspiration, and woody canopy cover to predict herbaceous vegetation cover (Figure 3.3). Precipitation and woody canopy cover were negatively correlated with herbaceous vegetation while evapotranspiration had a weak positive relationship. Overall, precipitation had the strongest correlation with herbaceous vegetation cover.

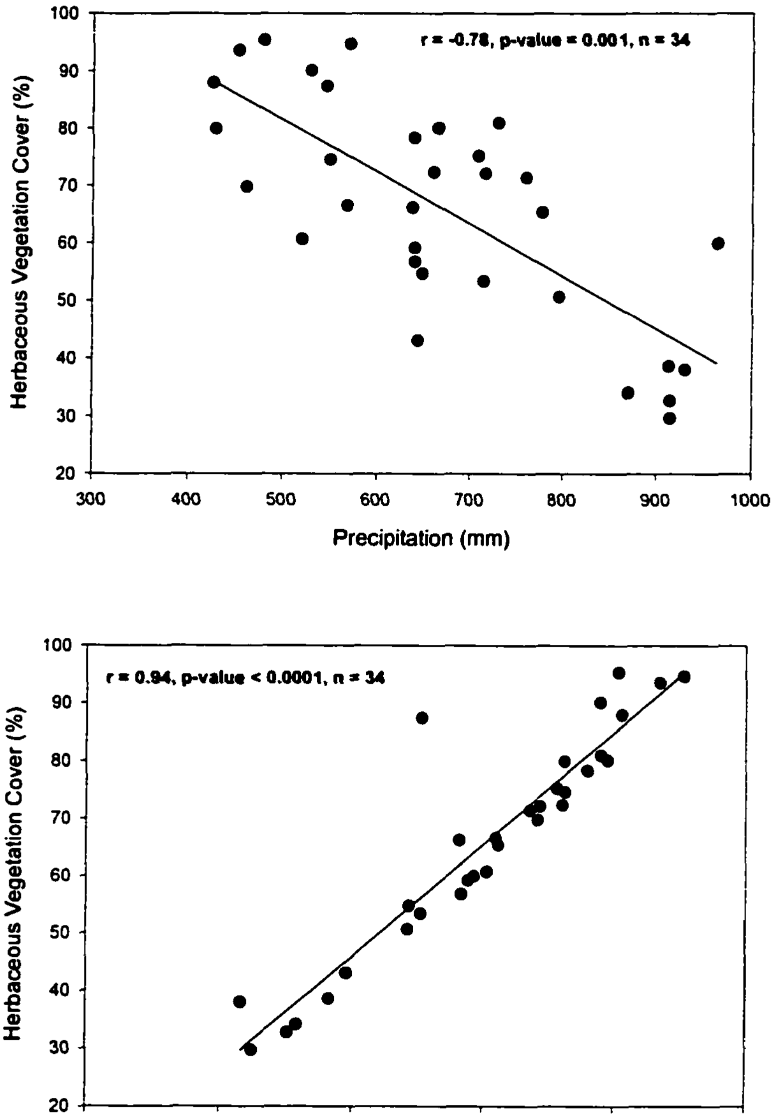

Figure 3.1a and 3.1b. Mean annual precipitation was negatively correlated with percent herbaceous vegetation cover (r = -0.78, p-value = 0.001, n = 34) and percent grass cover comprised the majority of total herbaceous vegetation cover (r = 0.94, p-value < 0.0001, n = 34).

Table 3.1. Correlations between density of trees per hectare of size class I = trees < 1 m tall, trees size class II = trees 1-3 m tall, trees of size class III = trees > 3 m tall, and all trees combined with precipitation, herbaceous vegetation cover and tree canopy cover.

	Tree < 1 m	**Trees 1-3 m**	**Trees > 3 m**	**All Trees Combined**
Precipitation	0.47*	0.46*	0.66*	0.67*
Herbaceous Vegetation Cover	-0.27	-0.62*	-0.62*	-0.55*
Woody Canopy Cover	0.01	0.68*	0.86*	0.63*

*** p-value < .05 significance**

Canonical correspondence analysis was used to assess tree species distributions between and within families in relationship to climate and soils properties (Figure 3.4). Variables included in the analysis were precipitation, potential evapotranspiration, elevation, slope, soil cation exchange capacity, pH, and electrical conductivity. The Fabaceae family in this system is mainly comprised of species from the Acacia genus with the exception of Albizia species. Acacias were associated with lower precipitation, lower evapotranspiration, lower cation exchange capacity and higher elevation zones. At the higher precipitation zones, the representation of different families of trees, including broad leaf trees species emerges. Overall, canonical correspondence analysis only explained 12.3 percent of the variation seen in tree family and species distributions indicating that very little effects of soil and climate.

When examining the proportion of plots that contained trees in each precipitation zone of the 328 subplots in the precipitation zone of less than 500 mm MAP, trees occurred in only five plots (Figure 3.5). The frequency of trees increased with increasing precipitation. The highest frequency of trees occurred in the 600-700 mm precipitation zone and > 900 mm precipitation zone (> 95 % of the subplots sampled had trees).

Trees belonging to the family Fabaceae comprised over 80 % of all trees under 700 mm precipitation, 70% of all trees under 800 mm precipitation and 60 % of all trees under 900 mm precipitation (Figure 3.6). In the highest rainfall zone, tree species were evenly distributed between four dominant families; Combretaceae, Ebenaceae, Euphorbiaceae, and Fabaceae.

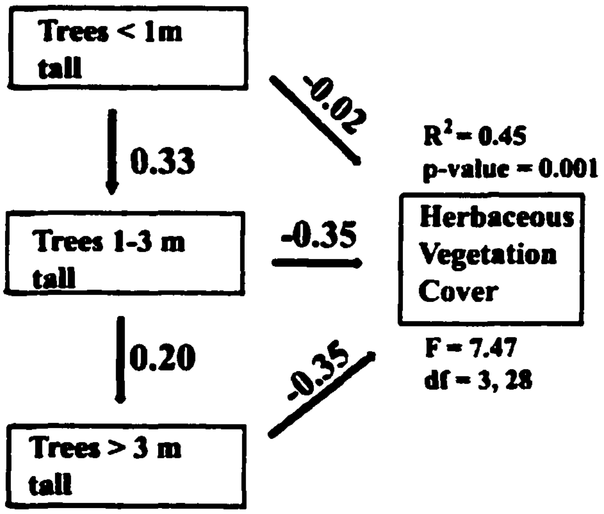

Figure 3.2. Path analysis was used to examine relationships between density of trees at the three different height classes. Trees of all size classes had negative interactions with herbaceous vegetation cover but taller trees had stronger negative correlations.

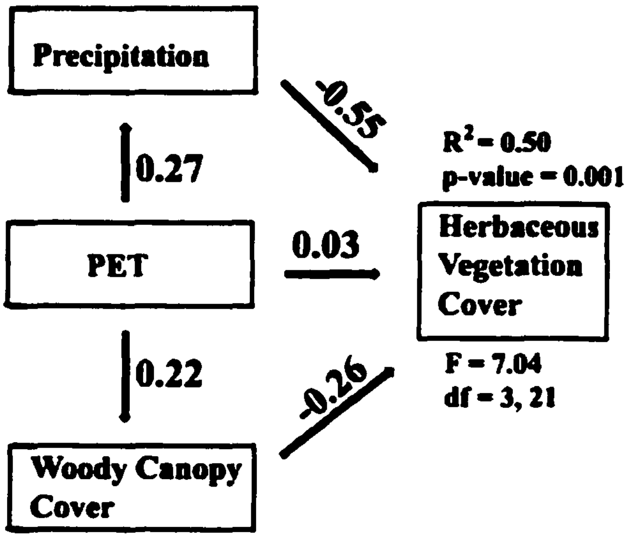

Figure 3.3. Path analysis determined that precipitation and woody canopy cover, which is correlated to taller trees, are negatively correlated with herbaceous vegetation cover while potential evapotranspiration and woody cover had a weak positive correlation.

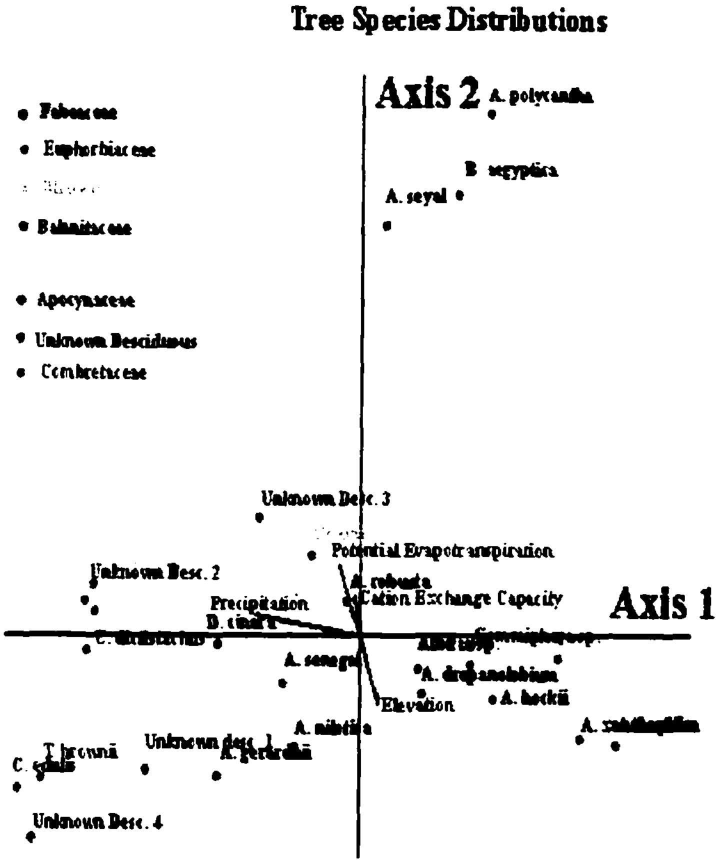

Figure 3.4. Canonical correspondence analysis of tree families and species with precipitation, soil cation exchange capacity, elevation, and potential evapotranspiration. Axis 1 accounted for 9.4 percent of the variation, and axis 2 and axis 3 accounted for the remaining 2.8 percent, indicating tree family and species distributions are not significantly

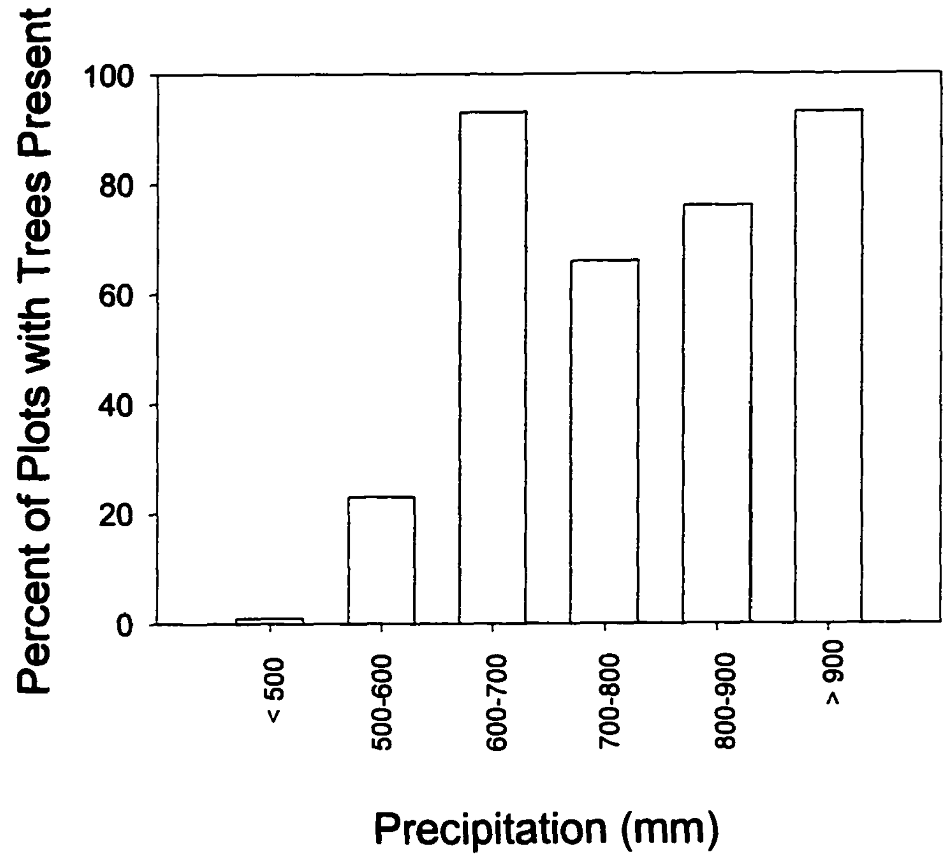

Figure 3.5. If a plot contained a tree it was counted as a 'treed' plot. This graphs shows the proportion of 'treed' plots per precipitation zone. Trees were found in only 5 plots out of a total of 328 plots in areas that receive less than 500 mm mean annual precipitation.

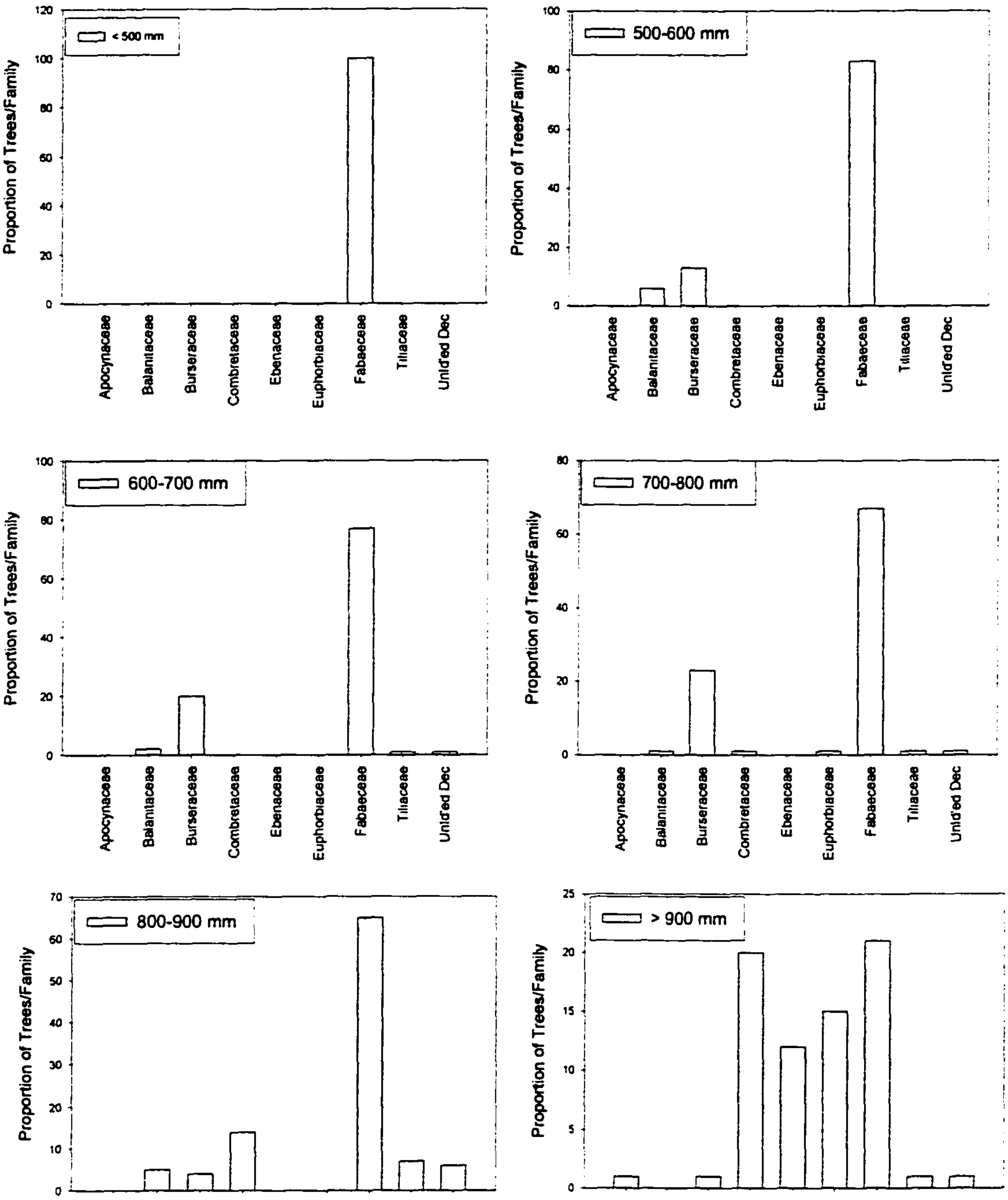

Figure 3.6. Percent composition of families at the different precipitation zones.

3.4 Discussion

Below 500 mm mean annual precipitation, the Serengeti is a true “grassland” where trees are essentially absent from the landscape. The grassland transitions into a “savanna grassland” where grass still is the dominant plant form, but distantly spaced trees are present. Above 700 mm of precipitation the landscape would be described as a “tree savanna’ where trees become the dominant growth form. Family and species composition changed along the precipitation gradient. Below 900 mm precipitation, Fabaceae was the dominant family comprising over 60% of all tree species in the sampled plots. Over 900 mm precipitation, the tree species were evenly divided between four families: Combretaceae, Ebenaceae, Euphorbiaceae, Fabaceae, yet Fabaceae still comprising over 20% of the tree species found in the sampled plots. Canonical correspondence analysis grouped both the families and species of trees with respect to the available climate and soil properties, but was able to explain only 12.3 percent of the variation. Thus, while patterns are apparent in this system, very little of the variations in species distributions are explained by the factors used in this analysis. Other factors could play more significant roles, particularly disturbance. Herbivory and fire are prevalent disturbance agents in this ecosystem and there is a need for further studies of their effects on tree distributions.

Facilitation between grasses and trees has been shown to be important in tree recruitment and establishment while herbivory and fire are negatively influential as they increase seedling and tree mortality (Dublin 1995). The mechanisms that influence seedling establishment and success are very different from the mechanisms that allow trees to persist and grow to taller height classes (Dublin and Sinclair 1990, Sinclair 1995). Tree-grass interactions in savanna ecosystems are very complicated and can not be predicted by simplistic models involving precipitation alone (Belsky 1990). Yet, interesting relationships with precipitation and vegetation structure did emerge in this study. Tree density and height were positively correlated with precipitation. As precipitation increased, tree density increased which in turn increased the number of trees in all size classes.

There is often a strong, negative correlation between tree density and grass cover in savannas (Bojorquez-Tapia et al 1990). The negative effects of trees on grasses can be the result of a variety of mechanisms such as canopy shading and under-story litter accumulation which affect light interception, germination, and tillering of grasses. Trees can influence the biogeochemistry of the soils surrounding the canopy (Bernhard-Reversat 1982, Georgiadis 1989) which in turn affects grass establishment and persistence. In the Serengeti, tree density and size increased and herbaceous vegetation decreased with increasing precipitation. Density of trees smaller than one meter in height was independent of herbaceous vegetation cover indicating that small trees may not be interacting or competing with herbaceous vegetation. As herbaceous vegetation cover decreased, total tree density increased but this was more an effect of the contribution of tree density at taller size classes. Larger individuals are most likely better competitors than smaller individuals because they have larger and more developed canopies and root structure. In this ecosystem, larger trees were more prevalent at higher rainfall zones and strong negative correlations were found between woody canopy cover and herbaceous cover, and between density of trees greater than three meters in height and herbaceous vegetation cover. Path analysis of the densities of trees in differing height classes showed the densities of trees in all size classes affected the amount of herbaceous vegetation but the density of larger trees was more strongly correlated with herbaceous vegetation cover.

Path analysis showed strong interactions between precipitation and woody canopy cover in their effects on herbaceous vegetation cover. This is consistent with a potential trade-off between the beneficial and negative effects of trees on grasses at different rainfall levels. At low precipitation, trees attenuate radiation, heat, and soil moisture stress such that competitive effects from trees are offset. As precipitation increases, the benefits obtained by herbaceous vegetation from trees are lost and competition for light becomes a limitation on herbaceous production. Competition between trees and grass has been shown to be more influential at higher rainfall sites (Belsky 1994) thus resulting in the interaction between precipitation and increased woody canopy cover in this system. The patterns found in this study are consistent with the hypothesis that tree size and precipitation are more influential than absolute tree density in determining herbaceous vegetation cover. It is impossible to draw conclusions as to the role that facilitation and competition may play in this system without an experimental approach, but the patterns reported in this study are consistent with the hypothesis that facilitation between grass and trees is important at lower precipitation zones, while competition between grasses and trees is more important at higher precipitation zones (Scholes and Walker 1993, Belsky 1994, Scholes and Archer 1997).

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CONCLUSION

The topics of this dissertation range from applied questions that are addressed to issues facing the Serengeti ecosystem to theoretical ecological questions that will contribute to our understanding of biodiversity and species richness patterns in many ecosystems.

I was interested in taking a closer look at potential differences in vegetation structure and diversity across two different land use areas. It was found that changes in grazing density at different times of the year (from wet season only to year around grazing) are correlated to differences in the vegetation structure. No differences in diversity were determined between the two areas, but increased forb, decreased grass cover and increased bare ground were associated with higher densities of ungulates throughout the year. This study determined that vegetation diversity was similar in both land use areas, indicating that the change in grazing and ungulate densities on the short grass plains may not be negatively impacting plant species' ability to persist. Yet density of grazers during the dry season may be negatively impacting vegetation structure, indicating that the timing of grazing might have important implications for grassland integrity. Because conclusions drawn from comparative studies are limited, a more experimental approach now needs to be undertaken to determine possible mechanisms for these observed patterns.

Modified-Whittaker plots were used in order to examine species richness patterns along a water availability and productivity gradient. Species richness increased with increased water availability and primary production at the 1000 m^2 plot and the regional scale but was uncorrelated when examined at the 1 m^2 subplot level. 1 m^2 subplot richness and the 1000 m^2 plot richness were positively correlated, indicating that species pool assemblages are detectable even at small scales. Yet only a small amount of variance was explained with the spatial analysis. Using the multi-scaled data from the modified-Whittaker plots, species area curves were calculated for each site. At higher water availability and production sites the slopes of the species area curves are steeper, suggesting that species accumulate at faster rates at these sites. Processes such as water availability and production potentially act at larger scales. However, small plots are commonly used in many studies targeted at determining the relationship between variables such as production and species richness. Relationships determined from this study point out that different processes might be acting at different scales.

Chapter 3 examines the savanna vegetation structure and compositional changes along the precipitation gradient. It was found that below approximately 500 mm mean annual precipitation trees are essentially absent from the landscape. Above this threshold trees appear on the landscape and the species composition is primarily dominated by

Acacia species. As precipitation increases, not only do trees occur more frequently, but they also become larger. This coincides with a decrease in the herbaceous vegetation as precipitation increases. On the other precipitation extreme of the system, above 900 mm of rainfall, the composition of trees is more evenly distributed between four different families, including the occurrence of broad leaf species. Canonical correspondence analysis determined relationships between vegetation composition with environmental variables such as precipitation, cation exchange capacity, potential evapotranspiration and soil variables. Although clear grouping of species was achieved, the environmental variables were only able to explain 12.7% of the variance of species composition. Variables that are difficult to quantify, such as herbivore and fire impacts, are thought to contribute to patterns of savanna vegetation species composition in this system.

APPENDIX I-1: SPECIES LIST OF SNP AND NCA

Species list for Ngorongoro Conservatbn Area

Family	Genus	Species
Acanthaceae	Barleria	ventricosa
Acanthaceae	Dyschoriste	radicans
Acanthaceae	Hypoestes	forkalei
Acanthaceae	Justica	elliotii
Acanthaceae	Justica	exigua
Acanthaceae	Justica	matemensis
Acanthaceae	Justica	sp
Acanthaceae	Ruellia	patula
Agelepiadaceae	Pentarrhinum	insipidium
Aizoaceae	Hypertelis	sp
Aizoaceae	Zaleya	pentandra
Alliaceae	Zygadenis	nuttallii
Amaranthaceae	Achyranthes	schinzii
Amaranthaceae	Amaranthus	hybridus
Amaranthaceae	Cyathula	orthocantha
Boraginaceae	Cynoglossum	geometricum
Boraginaceae	Heliotropium	steudneri
Caryophyllaceae	Orymaria	cordata
Commelinaceae	Commelina	africana
Commelinaceae	Commelina	benghalensis
Compositae	Aspilia	mossambiscensis
Compositae	Aster	hyssopifolius
Compositae	Athroisma	psylliodes
Compositae	Emillia	coccinea
Compositae	Erlangea	cordifolia
Compositae	Hirpicium	diffusum
Compositae	Pluchea	monocephala
Compositae	Sphaeranthus	sp
Convolvulaceae	Ipomea	longituba
Convolvulaceae	Ipomea	mombassana
Cruciferae	Arabis	sp
Cruciferae	Erucastrum	arabicum
Cucurbitaceae	Cucumis	aculeatus
Cucurbitaceae	Cucumis	ficifolius
Cyperaceae	Cyperus	species
Cyperaceae	Cyperus	usitatus
Cyperaceae	Kyllinga	nervosa
Euphorbiaceae	Euphobia	inaequilatera
Euphorbiaceae	Phyllanthus	rotundifolius
Fabaceae	Acacia	species
Fabaceae	Acacia	tortilis

Fabaceae	Crotalaria	deflersii
Fabaceae	Crotalaria	rhizoclada
Fabaceae	Crotalaria	serengetiana
Fabaceae	Crotalaria	sp
Fabaceae	Crotalaria	spinosa
Fabaceae	Eriosema	parviflorum
Fabaceae	Indigofera	hochstetteri
Fabaceae	Indigofera	microcharoides
Fabaceae	Indigofera	species
Fabaceae	Indigofera	volkensii
Fabaceae	Rhynchosia	sp
Fabaceae	Rhynochosia	minima
Geraniaceae	Monsonia	angustifolia
Graminaceae	Andropogon	greenwayi
Graminaceae	Aristida	pilgeri
Graminaceae	Cenchurus	ciliaris
Graminaceae	Chloris	gayana
Graminaceae	Chloris	pycnothrix
Graminaceae	Cynodon	dactylon
Graminaceae	Dactyloctenium	aegyptium
Graminaceae	Digitaria	diagonalis
Graminaceae	Digitaria	macroblephara
Graminaceae	Digitaria	milanjiana
Graminaceae	Digitaria	scalarum
Graminaceae	Eleusine	multiflora
Graminaceae	Eragrostis	aulocoperma
Graminaceae	Eragrostis	heteromera
Graminaceae	Eragrostis	humidicola
Graminaceae	Eragrostis	racemosa
Graminaceae	Eragrostis	tenuifolia
Graminaceae	Eriochloa	nubica
Graminaceae	Harpachne	schimperi
Graminaceae	Microchloa	kunthii
Graminaceae	Panicum	atrosanguineum
Graminaceae	Panicum	maximum
Graminaceae	Pennisetum	clandestinum
Graminaceae	Pennisetum	mezianum
Graminaceae	Pennisetum	stramineum
Graminaceae	Setaria	species
Graminaceae	Setaria	verticillata
Graminaceae	Sporobolus	fimbriatus
Graminaceae	Sporobolus	ioclades
Graminaceae	Sporobolus	nervosus
Graminaceae	Sporobolus	spicatus
Graminaceae	Themeda	triandra
Graminaceae	Tragus	berteronianus
Labiatae	Leucas	bracteosa
Labiatae	Leucas	neuflizeana

Labiatae	Leucas	sp
Labiatae	Orthosiphon	sp
Liliaceae	Anthericum	pterocaulon
Liliaceae	Asparagus	racemosa
Liliaceae	Chlorophytum	macrophyllum
Malvaceae	Sida	ovata
Polygalaceae	Polygala	sphaenoptera
Polygonaceae	Oxygonum	sinuatum
Portulacaceae	Portulaca	quadrifida
Rubiaceae	Kohautia	aspera
Rubiaceae	Kohautia	caespitosa
Rubiaceae	Oldenlandia	scopulorum
Rubiaceae	Pentanisia	ouranogyne
Scrophulariaceae	Cycnium	tubulosum
Scrophulariaceae	Rhamhicarpa	montana
Solanaceae	Solanum	incanum
Verbenaceae	Lippia	javaniea
Verbenaceae	Lippia	ukambensis
Verbenaceae	Priva	curtisiae
Vitaceae	Cissus	quadrangularus
Zygophyllaceae	Tribulus	terrestris

Species List for Serengeti Natonal Park

Family	Genus	Species
Acanthaceae	Asystasia	verolcourt
Acanthaceae	Barleria	taitensis
Acanthaceae	Dyschoriste	radicans
Acanthaceae	Hypoestes	forkalei
Acanthaceae	Justica	betonica
Acanthaceae	Justica	elliotii
Acanthaceae	Justica	exigua
Acanthaceae	Justica	sp
Agelepiadaceae	Pentarrhinum	insipidium
Aizoaceae	Delosperma	nakurense
Aizoaceae	Hypertelis	sp
Alliaceae	Zygadenis	nuttallii
Amaranthaceae	Amaranthus	hybridus
Amaranthaceae	Cyathula	orthocantha
Anacardiaceae	Cannea	huimilis
Anacardiaceae	Sclerocarya	birrea
Asclepiadaceae	Strathmostelma	sp
Balanitaceae	Balanites	aegyptica
Boraginaceae	Heliotropium	steudneri
Burseraceae	Commiphora	trothae
Combretaceae	Combretum	molle
Commelinaceae	Commelina	africana
Commelinaceae	Commelina	benghalensis

Commelinaceae	Commelina	purpurea
Commelinaceae	Commelina	sp
Commelinaceae	Commelina	trilobosperma
Commelinaceae	Cynotis	sp
Commelinaceae	Murdannia	simplex
Compositae	Aspilia	mossambiscensis
Compositae	Aster	hyssopifolius
Compositae	Athroisma	psylliodes
Compositae	Berkheya	spekeana
Compositae	Bidens	sp
Compositae	Conyza	stricta
Compositae	Crabbea	velutina
Compositae	Emilia	javanica
Compositae	Erlangea	cordifolia
Compositae	Hirpicium	diffusum
Compositae	Klienia	gregorii
Compositae	Pluchea	monocephala
Compositae	Sphaeranthus	sp
Convolvulaceae	Convolvulus	sagittatis
Convolvulaceae	Ipomea	longituba
Convolvulaceae	Ipomea	mombassana
Cruciferae	Arabis	sp
Cucurbitaceae	Cucumis	ficifolius
Cucurbitaceae	Cucumis	sp
Cucurbitaceae	Momordica	foetida
Cyperaceae	Bulbostylis	boeckleriana
Cyperaceae	Bulbostylis	buchanani
Cyperaceae	Cyperus	usitatus
Cyperaceae	Fimbristylis	ovata
Cyperaceae	Kyllinga	nervosa
Cyperaceae	Obtusifloris	vahl
Cyperaceae	Pycreus	sp
Euphorbiaceae	Euphobia	inaequilatera
Euphorbiaceae	Phyllanthus	maderaspatensis
Euphorbiaceae	Phyllanthus	rotundifolius
Euphorbiaceae	Phyllanthus	sp
Fabaceae	Acacia	drepandilobium
Fabaceae	Acacia	species
Fabaceae	Acacia	tortilis
Fabaceae	Acacia2	species2
Fabaceae	Albizia	harveyi
Fabaceae	Cassia	fallacina
Fabaceae	Chaemacrista	falacina
Fabaceae	Chamaecrista	kirkii
Fabaceae	Chameasta	sp
Fabaceae	Crotalaria	deflersii
Fabaceae	Crotalaria	laburnifolia
Fabaceae	Crotalaria	rhizoclada

Fabaceae	Crotalaria	serengetiana
Fabaceae	Crotalaria	sp
Fabaceae	Eriosema	montanum
Fabaceae	Eriosema	parviflorum
Fabaceae	Glycine	wightii
Fabaceae	Indigofera	basiflora
Fabaceae	Indigofera	hochstetteri
Fabaceae	Indigofera	microcharoides
Fabaceae	Indigofera	vohemanensis
Fabaceae	Indigofera	volkensii
Fabaceae	Medicago	caciniata
Fabaceae	Tephrosia	linearis
Fabaceae	Tephrosia	pumila
Fabaceae	Vigna	frutenscens
Fabaceae	Vigna	sp
Fabaceae	Zornia	setosa
Gentianaceae	Eniocosterma	axillare
Graminaceae	Andropogon	greenwayi
Graminaceae	Aristida	pilgeri
Graminaceae	Bothrichloa	insculpta
Graminaceae	Bothriochloa	radicans
Graminaceae	Cenchurus	ciliaris
Graminaceae	Chloris	gayana
Graminaceae	Chloris	pycnothrix
Graminaceae	Chrysochloa	orientalis
Graminaceae	Cynodon	dactylon
Graminaceae	Dactyloctenium	aegyptium
Graminaceae	Digitaria	macroblephara
Graminaceae	Digitaria	scalarum
Graminaceae	Elyonurus	argenteus
Graminaceae	Eragrostis	aulocoperma
Graminaceae	Eragrostis	racemosa
Graminaceae	Eragrostis	tenuifolia
Graminaceae	Eriochloa	nubica
Graminaceae	Eustachys	paspaloides
Graminaceae	Harpachne	schimperi
Graminaceae	Heteropogon	contortus
Graminaceae	Hyparrhenia	papillipas
Graminaceae	Hyperrhenia	anamosa
Graminaceae	Hyperthalia	dissoluta
Graminaceae	Microchloa	kunthii
Graminaceae	Oplismenus	comprilus
Graminaceae	Panicum	atrosanguineum
Graminaceae	Panicum	maximum
Graminaceae	Pennisetum	clandestinum
Graminaceae	Pennisetum	mezianum
Graminaceae	Pennisetum	stramineum
Graminaceae	Setaria	sphacelata

Graminaceae	Sporabolus	carpensus
Graminaceae	Sporobolus	fimbriatus
Graminaceae	Sporobolus	ioclades
Graminaceae	Sporobolus	nervosus
Graminaceae	Sporobolus	pellucidus
Graminaceae	Sporobolus	spicatus
Graminaceae	Themeda	triandra
Graminaceae	Trachypogon	spicatus
Graminaceae	Tragus	berteronianus
Labiatae	Becium	sp
Labiatae	Fuerstia	africana
Labiatae	Leucas	neuflizeana
Labiatae	Leucas	sp
Labiatae	Ocimum	suave
Labiatae	Orthosiphon	suffrutescens
Liliaceae	Anthericum	pterocaulon
Liliaceae	Asparagus	falcatus
Liliaceae	Asparagus	racemosa
Liliaceae	Bulbine	abyssinica
Liliaceae	Chlorophytum	bakeri
Liliaceae	Chlorophytum	macrophyllum
Liliaceae	Chlorophytum	sp
Malvaceae	Abutilon	mauritianum
Malvaceae	Hibiscus	flavifolius
Malvaceae	Melhania	ovata
Malvaceae	Sida	alba
Malvaceae	Sida	cuneifolia
Malvaceae	Sida	ovata
Nyctaginaceae	Commicarpus	pedunculosus
Polygalaceae	Polygala	sphaenoptera
Polygonaceae	Oxygonum	sinuatum
Portulacaceae	Portlaca	foliosa
Portulacaceae	Portulacca	sp
Portulacaceae	Talinum	portulacifolium
Rubiaceae	Kohautia	aspera
Rubiaceae	Kohautia	caespitosa
Rubiaceae	Pentanisia	ouranogyne
Scrophulariaceae	Craterostigma	plantagineum
Scrophulariaceae	Cycnium	tubulosum
Scrophulariaceae	Striga	asiatica
Solanaceae	Solanum	incanum
Verbenaceae	Lippia	javaniea
Verbenaceae	Priva	curtisiae
Vitaceae	Cyphostemma	nieriensis
Zygophyllaceae	Tribulus	terrestris