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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

The Effect of Spatial Heterogeneity and Environmental Gradients on Vegetation in a Semi-arid Environment: Black Mesa, Cimarron County, Oklahoma

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

Doctor of Philosophy

By

Mark Richard Micozzi

Norman, Oklahoma

2001

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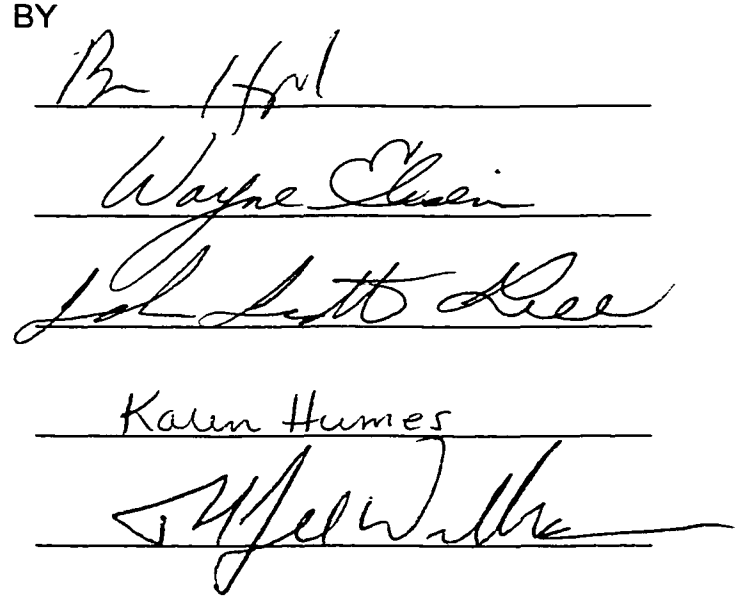
The Effect of Spatial Heterogeneity and Environmental Gradients on Vegetation in a Semi-arid Environment, Black Mesa, Oklahoma

A Dissertation APPROVED FOR THE
DEPARTMENT OF GEOGRAPHY

BY



ACKNOWLEDGEMENTS

Before I acknowledge the many individuals and agencies that have supported my research at Black Mesa, I would like to dedicate this dissertation to Annette, my cousin who has battled diabetes while finishing her medical degrees, my Mom, who always guided me from the brightest star in the heavens, and my Dad, who guided my on earth.

I arrived in Norman in the midst of the Oklahoma City bombing in 1995 and quickly learned what was mean by the "spirit of Oklahoma." Nowhere else have I experienced the outpouring of friendship, compassion and a helping hand than in this state. The same is true of a small part northwest Oklahoma, a relic landscape in the middle of what many locals call "God's country." It was after I discovered Melany (wife to be at the time) and after a failed research campaign in the Grand Teton National Park in Wyoming, that I stumbled on my study area, Black Mesa. At the same time that is was a new beginning for me it was also a new beginning for Monty Joe and Vicki Roberts at their newly crowned "Black Mesa Bed and Breakfast" (at the foot of Black Mesa). What started out as a business deal for me turned out to be a start of a wonderful friendship for my family and me.

We learned about homesteading and ranching, wind and rain, dinosaurs and plants, basalt and sandstone, people and history, togetherness and a helping hand and surviving in the desert. We found the heart and soul of a God-fearing people and what it means to live a strong commitment to faith.

On a landscape that some may seem as formidable, I see as welcoming. As a geographer, I immersed myself in the history of Black Mesa and realized that research doesn't always begin with books, numbers or statistics but with people. Thus, I have given credit to many individuals below and since it was my goal to become multi-disciplinary in my studies, I have learned more about my field so as to pass on knowledge to others. The desire to learn and teach never ends.

First, I would like to thank the Nature Conservancy, NASA EPSCOR (Experimental Program to Stimulate Competitive Research) and the Graduate College and Graduate Student Senate at the University of Oklahoma for financial support. Research requires funding and I am indebted to these agencies and institutions. Thank you.

The vegetation portion of my research required the use of both public and private lands. I would like to thank the Nature Conservancy, Black Mesa State Park and the Kenton ranchers for permission to climb the Mesa numerous times a day. I think nine is the record but hey, who's counting? I would also like to thank the personnel at the Oklahoma Biological Survey and Bebb Herbarium for supplying field equipment and species identification assistance and storage. I often thought about spending quality time with smashed plants and now I have accomplished it. How cold does it have to be to keep the plants from walking out of the Herbarium?

For the soils-related portion of my research I turned to the Natural Resources Conservation Service and the help of Robert McBride, Greg Scott, Troy Collier and Carl Woods. They supplied soil manuals, field designs, professional assistance, soil data and publications. I thank all of them for their time and patience teaching me about "dirt." I would also like to thank Wayne Furr and Neil Suneson at the Oklahoma Geological Survey for their knowledge about Black Mesa and various sources of geologic data and publications. Thank you Wayne for being a firm believer in making a good map and the importance of scale. A significant component to my research was due to the help of Dr. Hailin Zhany and his staff at the Soil, Water, and Forage Analytical Laboratory at Oklahoma State University. They were instrumental in completing the texture and fertility analysis at an affordable rate and in a timely and professional manner. Thank you.

There is no better place to study dynamic climatic effects as in Oklahoma. I owe my meteorological portion of the dissertation to John Ensworth and his resourcefulness. He was instrumental in setting up the "mesanets" at Black Mesa. We lugged equipment on and off the Black Mesa many times trying to figure out the best way to record data for both of our dissertations. Our shared interest in Black Mesa strengthened our belief in collaborative efforts. John was able to donate (with help from the Environmental Verification Analysis Center at the University of Oklahoma) rain and temperature equipment and secure a place to calibrate our instruments (thanks to the Oklahoma Mesonet staff).

When the tough got worse, John got tougher. I cannot recall the numerous set-ups and tests we did before we got it right. I have never met a person with more knowledge about so many things. He brought the heavens of Black Mesa to the ground with his "mega telescope." Thank you John for your hours of work and help driving to Black Mesa. Additional thanks goes to Bill Beams from the National Weather Service in Amarillo, Texas for auxillary climate data.

I certainly couldn't study Black Mesa without a bit of history under my wing. I would like to thank the staff at the Cimarron Heritage Center in Boise City, the Chamber of Commerce in Kenton and numerous Kenton ranchers for historical data and a "sense of place." I now know what "place" means to a geographer's landscape. I want to thank Rebecca Scott and former director Dr. Lee Williams and staff at the Oklahoma Alliance for Geographic Education (OKAGE) for promoting geographic teaching and research at Black Mesa.

I want to express my gratitude to Deon Perkins, the Black Mesa State Park Ranger, for all his time, muscle and support implementing and carrying out my research needs. Access to land was made easier with your help. Until this day I still don't know how someone could bust a tail bone on the top of Black Mesa.... maybe it was the gallons of water I made you carry to calibrate the instruments. Thank you Deon and staff for your cooperation and willingness to serve my special needs.

I would like to thank my committee members (Dr. Bruce Hoagland, Dr. Lee Williams, Dr. Karen Humes, Dr. Scott Greene and Dr. Wayne Elisens) for making my experience smooth and enjoyable. I chose carefully, wisely and correctly! I was so lucky to have a stable platform on which to work. I owe my current knowledge of biogeographic principles and vegetation science to my advisor, Bruce Hoagland, who took me under his care when I asked him "...what can I do at Black Mesa?" He had all the answers and never led me in the wrong direction. I trusted him from day one and he never let me down. I remember the first day of field sampling and identification (hot, no shade, a bunch of Latin, little water and our prickly plant friends) to the time he left me on my own to discover the perils of field work and the glamour of "learning by doing." Of course I can't forget the time he fell into the "big daddy cholla"...how many of those things did we pick out? Thank you Bruce for all your time and patience molding me into one of your Hoagland's Heros!

I want to thank my family back East, especially my Dad for never losing site of my goals. You have been more than a phone call away and knowing that you invested interest in my career makes it all worth it. I feel that you have sent me in your footsteps of academia, good teaching and sound morals, especially in the classroom. Truth, fairness and honesty will always be there. I love you.

To my "Kenton family" at Black Mesa, I can't express how smooth you made my research flow, especially under the care of Monty Joe and Vicki Roberts (and family) at the Black Mesa Bed & Breakfast. I met so many family members and friends that made my visits special and each one had something new for me to obsorb. Everyone was always so kind. I firmly believe that I would still be on the Mesa if I did not have the opportunity to carry out my research from your cozy ranch with a beautiful view.

We helped each other as we started something new, my research and your business. After my first stay, business turned into friendship and my monthly visits became a ritual, especially bringing back "all that grass." I cannot begin to list the numerous times that you have helped me see the end to my sampling. Cool summer nights, a cozy winter fireplace, a breakfast fit for climbing, prickly pear syrup, home-cooked meals and homemade desserts, a drive instead of a hike, reading gages, meeting new guests, watching the rain, cattle ranching, sunscreen, family events, relaxing conversation, star searching, the bright red roof and many laughs to last forever. What will I remember the most? I will remember how our families grew together with every visit and we enjoyed one of God's greatest gifts, the love of friendship. God bless you and your wonderful home. Memories last forever.

To my family in Norman...we have grown together over the past four years and you have seen me through the roughest and smoothest roads to this day. Research takes time and that time is over. Casey and Chelsea, you have been my pleasure and reality-check throughout this process. We have learned together and made our house a home during our time together. I would not trade the times you made me realize that helping you and being with you was worth more than one line of written text of another journal article. We learned to experience real life issues and take care of our precious love for one another. We started something wonderful, and with your mom, we moved through life as a close family. I hope that our times together have made you grow in a positive way and that all your dreams do come true.

Ending with the best thing that has ever happened to me, my marriage to the most understanding, loving and beautiful wife, Melany. There isn't a phrase or word I could use to express what you have meant to me, except for these...*I love you*. You have been the rock by my side when I needed a place to lean and the inspiration I needed to finish my dissertation. When the end never seemed to show itself, you were patient and supportive. You never lost sight of my goal and the reason I wanted a PhD. It strengthened our love when others said it wouldn't. It made us stronger and closer despite the long hours apart. It taught us that a family could remain happy in difficult times because we care so much for each other and our kids. We made it happen together.

I can't recall the numerous times that you stared at the back of my head, you in bed and me burning the midnight oil at the computer. Those days are over and my work is finished. Throughout this dissertation, we have enjoyed so many things together and so much more lies in the future. We have a lifetime together that God has given us. Your kindness, love, support and faith in our life together are never under appreciated. I know that without you, this day would not have come. I love you so much and may our love grow as the never-ending wind that crosses Teton Pass and the dock that sits on Jackson Lake.

Sincerely,

Marco

PREFACE

This dissertation was written in three chapters. The first chapter is an introduction to general concepts related to the overall objectives. The subsequent two chapters present the research results and are written for submission to the journals *The Professional Geographer* and *Journal of Vegetation Science*.

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Chapter 1

Introduction

The research presented in this dissertation focuses on a small part of the Mesa de Maya Plateau called Black Mesa. Situated in the far northwest corner of Cimarron County, Oklahoma, this semi-arid environment is among the state's most topographically complex and botanically unique areas. The change in topography at Black Mesa from the surrounding plains is very abrupt and so distinctive that Blair and Hubbell (1938) defined this biotic district in northwest Oklahoma as the "Mesa de Maya District." As Rogers (1954) states, "one cannot help but be impressed by the abrupt change in the vegetation...when approached from the nearly unbroken stretches of grassland to the east." The flora of Black Mesa lies at a crossroads defined by four major biomes that contribute to the local species richness and diversity. In fact, portions of the easternmost extension of the Rocky Mountain Foothill vegetation and the westernmost extension of the Eastern Deciduous Forest occur at Black Mesa (The Nature Conservancy 1998).

The first systematic botanical research in the Black Mesa region was a dissertation by Claude M. Rogers in 1949 (*The vegetation of the Mesa De Maya region of Colorado, New Mexico, and Oklahoma)*. He classified nearly six hundred species of plants, documented their level of dominance and mapped the vegetative species into four broad classes: prairie, foothill, Rocky Mountain and riparian. Rogers (1949) insisted that further divisions within each of these classes based on dominant species was needed, but that Mesa de Maya covered such a large area that the process would be "...unwieldy." Rogers (1953) also stated that "...the Mesa de Maya region is a unique geographic entity...but since it is located in the extreme corners of three states, it is

significant that certain species are only found in one or more of these states in a particular region." Because of the great distance from research institutions and populated towns, little is known about the distribution and abundance of plant species at Black Mesa.

In an attempt to increase the floristic knowledge of the region and awareness of prairie ecosystems, Clark (1996) conducted a floristic survey of the Mesa de Maya in Las Animas County, Colorado. She recorded 570 plant species grouped into the same four classes used by Rogers (1949). The research presented here encompassed about 18 sq km and included 159 plant species classified into nine distinct vegetation associations. In conjunction with technological advancements in computer technology (geographical information systems, remote sensing and multivariate statistical techniques), this research is a natural continuation of Rogers' research (1949) and incorporates contemporary trends in biogeography, applied ecology and vegetation science.

Chapter 2

Spatial heterogeneity is considered by several authors to be the single most important factor regulating the distribution of species (Wiens 1976; Urban et al. 1987; Pollock et al. 1998; Huston 1994). Risser (1987) defines spatial heterogeneity as the degree of dissimilarity over a given aerial extent. Landscape heterogeneity, defined by the degree of spatial heterogeneity, is heavily influenced by geomorphology and topography (Hack and Goodlett 1960; Pastor et al. 1982; Swanson et al. 1988). Finally, vegetation heterogeneity, which is directly related to landscape heterogeneity, is the degree of dissimilarity

of species distribution over a given aerial extent. Given these definitions, vegetation heterogeneity is controlled by landscape heterogeneity and as landscape heterogeneity increases, so does species richness and diversity (MacArthur 1965; Forman and Godron 1986; Malanson 1993; Gould and Walker 1997; Grace and Pugesek 1997; Mourelle and Ezcurra 1997; Tilman 1997; Von Numers and Van der Maarel 1998; Gould and Walker 1999). Research involving spatial heterogenety provides ecologists and biogeographers the opportunity to study the relationships between the organization of the physical landscape and species composition, richness and diversity.

Geomorphic and topographic factors play an important role in creating spatially complex landscapes and regulating species composition, richness and diversity (Whittaker 1956; Hack and Goodlett 1960; Ward et al. 1993; Wondzell et al. 1996; Bridge and Johnson 2000). These factors increase landscape heterogeneity and promote natural habitat fragmentation (Forman and Godron 1986). Fragmentation, a product of natural processes and anthropogenic activities, produces a landscape mosaic of interacting patches or polygons on a map coverage (Risser 1987; Turner 1989; Forman 1995). Consequently, landscapes with more diverse habitat structure, combined with an unequal distribution and flow of resources, tend to contain greater species richness and diversity (Tilman 1982; Forman and Godron 1986; Schluter and Ricklefs 1993). Few studies involving landscape heterogeneity have focused on natural fragmentation and its influence on species composition, richness and diversity.

Studies involving heterogeneous landscapes have focused on patterns of vegetation distribution and species richness and diversity in relation to various

biotic and abiotic factors at various scales (Ward et al. 1993; Grace and Pugesek 1997; Hoagland and Collins 1997; Hsieh et al. 1998; Vázquez and Givnish 1998). Additionally, the interaction between landforms, geomorphic processes and soils often determine the distribution of plant communities and patterns of species richness and diversity (Parker 1991; McAuliffe 1994; Pérez 1994; Wondzell et al. 1996). These studies, and others, have focused on the effect of the environment on species distribution and/or species richness and diversity at one scale and research involving species richness and diversity related to spatial heterogeneity at various scales is lacking. Studying how species richness and diversity is structured on a landscape at different scales provides a more accurate approach to measure and monitor patterns and change in biodiversity (Cox and Larson 1993; Valverde et al. 1996; Gould and Walker 1997). Although many studies have demonstrated that species richness and diversity are distributed differently among scales, there is a lack of research involving the resulting spatial patterns of species richness and diversity among scales.

The most common hypothesis used in several studies attempting to understand patterns of species richness and diversity is the intermediate disturbance hypothesis (IDH). The IDH predicts that species richness or diversity is maximized by intermediate levels of environmental disturbance or stress (Grime 1973; Connell 1978; Huston 1979). It was first applied to herbaceous communities (Grime 1973; Al-Mufti 1977) and marine environments (Ward and Stanford 1983; Wilson and Keddy 1988; Gough et al. 1994) where the highest species richness and diversity was measured at intermediate levels of biomass, a surrogate for productivity. More recently, the IDH concept has become an

important component of research relating species richness and diversity to spatial heterogeneity and habitat structure (Noy-Meir 1985; Montaña 1990; Gould and Walker 1997). For example, literature in shoreline gradients (Wilson and Keddy 1988; Wisheu and Keddy. 1989) and dry environments (Montaña 1990; Valverde et al. 1996) suggest that species richness and diversity adhere to variations on the IDH at different scales.

Understanding how species richness and diversity is structured on a landscape at different scales can help solve ecosystem management issues (Scott et al. 1993; Scott and Csuti 1997; Driese et al. 1997; Hong et al. 1998). Since many issues are based on sustainability, a basic principle of ecosystem management (Franklin 1997), understanding species distributions and factors that increase or decrease species richness and diversity is crucial for successful management at all scales (Forman 1990; Zonneveld and Forman 1990; Brosofske et al. 1999).

Traditionally, the broad aims and objectives of conservation operated on a species-based approach. A recent shift towards landscape diversity level research with a landscape-ecosystem-specific approach restores ecosystems and landscapes to a state that is close to their original structure, function and dynamics (Franklin 1993; LaRoe 1993; Lapin and Barnes 1995; Brunner and Clark 1997; Flather et al. 1998; Leser and Nagel 1998; Brosofske 1999). This holistic (ecosystem) approach revitalizes the natural dynamics of ecosystems and insures sustainability of resources (Naveh and Lieberman 1994; Leser and Nagel 1998). Linking local level vegetation research with landscape level conservation provides ecosystem managers with accurate maps that can serve

as a basis for planning and management (Noss 1983; O'Neill et al. 1988; Agee 1988; Haber 1990; Scott and Csuti 1997). Studies that map and seek to understand the structure of a landscape at various spatial scales can provide valuable information for planners and managers involved with holistic approaches to conservation.

The main goal of chapter 2 is to evaluate the effect of spatial heterogeneity at the landscape and sub-landscape scale on the distribution of vegetation at Black Mesa, a spatially complex and naturally fragmented landform. More specifically, it focuses on how species richness and diversity and its pattern are related to vegetation composition, geomorphology and topography, and landscape structure at the landscape and sub-landscape scale. It is hoped that the results of this research will add to a growing body of literature, which focuses on how species richness and diversity respond to different levels of spatial heterogeneity at different scales.

The research presented here demonstrated that the effect of spatial heterogeneity at the sub-landscape scale had the most impact on species richness and diversity. Increased spatial heterogeneity and habitat fragmentation were defined by an increase in the number of patches and total edge and smaller patch sizes. Increased slope, rock cover and medium to large rocks, which proved to be major factors increasing species richness and diversity, dictated the degree of spatial heterogeneity and fragmentation.

It was also determined that species richness and diversity appear to be affected by slight differences in size and amounts of surface rock. In addition, the greatest species richness and diversity is directly linked to intermediate levels

of spatial heterogeneity, defined by moderate habitat structure. These environments represent ecotones or transitional areas between two different environments. Outside of these transitional environments, species diversity increased in more spatially complex environments and species richness increased in less spatially complex environments. Intermediate levels of shrub abundance defined high levels of species richness and diversity. Intermediate levels of grass abundance and medium sized rockss also defined high levels of species diversity. It was shown that results from larger scale patterns of species richness and diversity contributed to the understanding of smaller scale patterns of species richness and diversity at Black Mesa.

Lastly, the production of vegetation and geologic maps from the research presented here demonstrated that the underlying spatial pattern of the geologic substrate is reflected in the broad patterns of vegetation. Additionally, surface geology, defined by rock cover and rock size better explain patterns of woody vegetation patterns at Black Mesa.

Chapter 3

Gradient analysis assists in the exploration of spatial patterns of vegetation and helps to build an understanding of the structure and composition of vegetation in terms of environmental factors called gradients (Whittaker 1967). When combined with ordination methods, gradient analysis aids in determining the varying degrees of similarity among samples (or species) and how they are correlated with environmental gradients (Gauch 1982; Kent and Coker 1992). Ordination means "to set in order" (Kent and Coker 1992) and the "order" is the

"...arrangement of vegetation samples in relation to each other in terms of their similarity of species composition and/or their associated environmental factors (Kent and Coker 1992)." Objects close in the ordination space are generally more similar than objects distant in the ordination space.

Environmental gradients are commonly used for analyzing spatial patterns of vegetation and the relationship between vegetation and the environment (Kent and Coker 1992; Jongman et al. 1995). The ability to summarize and classify ecological patterns has increased with the development of multivariate techniques (Gauch 1982; Keddy 1991; McGarigal et al. 2000). These techniques are related to direct and indirect gradient analysis, two primary methods for the study of species response along environmental gradients. Indirect gradient analysis, typically referred to as unconstrained or vegetation ordination, originated in the 1950s by Curtis and McIntosh (1951) and Goodall (1954) and later refined by Bray and Curtis (1957) with the development of their polar ordination technique. Indirect gradient analysis is performed independently from the environmental factors and uses mathematical models to exploit the major underlying structure of the data in a few abstract dimensions by examining the variation within it (Austin 1985). One of the most widely used unconstrained ordination techniques is detrended correspondence analysis (DCA; Hill and Gauch 1980).

In contrast, direct gradient analysis (sometimes referred to as environmental ordination) was developed as a research tool by Whittaker (1948) and explores the distribution of species along known environmental gradients. More recently, canonical (constrained) ordination methods, referred to as

multivariate direct gradient analysis (ter Braak 1986; ter Braak and Prentice 1988), detect patterns of variation in species and environmental data. It represents a more efficient way of analyzing variation in community composition and structure than attempting to organize single species distributions with environmental factors as in true direct gradient analysis.

The main purpose of canonical ordination is to simplify the interpretation of complex data sets by organizing samples along gradients defined by combinations of interrelated variables (ter Braak 1987). These methods are designed to extract environmental gradients from large ecological data sets where the ordination axes are linear combinations of environmental variables (ter Braak and Verdonschot 1995). Canonical correspondence analysis (CCA; ter Braak 1986) is the best canonical ordination method that elucidates the relationships between species composition and the environment (ter Braak and Prentice 1988; McGarigal et al. 2000) and has become the most widely used gradient analysis technique (Palmer 1993; McCune 1997). Few studies have combined the use of both constrained (CCA) and unconstrained (DCA) ordination techniques (Allen et al. 1991; Velázquez 1994; Ferreyra et al. 1998). Using both techniques adds confidence to qualitative and quantitative analyses when interpreting significant compositional and environmental gradients.

In studies using multivariate analysis, the scale of the study will determine which gradients are analyzed to explain the variance in the data. Larger scale studies often focus on climatic or elevation gradients while smaller scale studies usually focus on topographic and edaphic factors. Multivariate direct gradient analysis has typically been employed in montane (Tang and Ohsawa 1997;

Ferreyra et al. 1998; Hsieh et al. 1998; Kirkpatrick and Bridle 1998; Vazquez and Givnish 1998) and arid environments (Cornelius et al. 1991; Parker 1991; McAuliffe 1994; Valverde et al. 1996). Given that montane environments contain larger scale landforms than arid environments, underlying gradients that account for most of the variation in species data are related to larger scale gradients. As noted in the literature, the effects of temperature, precipitation and insolation on vegetation along altitudinal gradients tend to be more significant in montane landscapes. In contrast, the effects of surface rock cover, soil texture and nutrient availability on vegetation along slope gradients tend to be more significant in arid and semi-arid landscapes.

The overall goal of chapter 3 is to analyze ecological patterns as related to environmental gradients at Black Mesa, situated in the far northwest corner of Cimarron County, Oklahoma. Additionally, this research will explore the main environmental factors contributing to patterns of species richness and diversity at the site level, adding to the general body of literature in arid and semi-arid environments. Analyses showed that temperature and precipitation at Black Mesa was not shown to be a major factor affecting the distribution of vegetation at the scale of analysis defined by this study. Instead, vegetation structure and composition at smaller scales were most affected by topography and geomorphology (slope, rock size, rock cover and sand content) and nutrient availability (nitrogen, phosphorus, potassium).

The greatest species richness and diversity was found in areas with moderate habitat structure containing a mixture of shrubland and grassland species. These environments contained medium sized rocks, moderate slopes

and moderate amounts of surface rock cover and nutrients. Increased habitat structure resulted in higher species diversity and decreased habitat structure resulted in higher species richness. In addition, the abundance of woody and tall grass species was mostly influenced by the presence of large rocks, increased slopes and soil texture and higher nutrient availability. The abundance of shorter and mixed grass species was mostly influenced by increased rock cover, soil depth and pH, finer soil texture and decreased rock size.

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Chapter II

The Role of Spatial Heterogeneity on Species Richness and Diversity at Black Mesa, Cimarron County, Oklahoma

Abstract

This research focuses on landscape level patterns in a semi-arid environment, which consists of mesas and canyons in northwest Oklahoma. Among the state's most botanically unique and topographically complex areas, it lies at a crossroads defined by four major biomes that contribute to the local species richness and diversity. The main goal of this research is to evaluate the effect of spatial heterogeneity at the landscape and sub-landscape scale on the distribution of vegetation at Black Mesa, a spatially complex and naturally fragmented landform. This research will focus on how species richness and diversity and its pattern are related to vegetation composition, geomorphology and topography, and landscape structure at the landscape and sub-landscape scales. It is hoped that the results of this research will add to a growing body of literature, which focuses on how species richness and diversity respond to different levels of spatial heterogeneity at different scales.

The research presented here demonstrated that the effect of spatial heterogeneity at the sub-landscape scale had the most impact on species richness and diversity. Increased spatial heterogeneity and habitat fragmentation at Black Mesa were defined by an increase in the number of patches, total edge and smaller patch sizes. Increased slope, rock cover and medium to large rocks, which proved to be major factors increasing species richness and diversity, dictated the degree of spatial heterogeneity and fragmentation.

It was also determined that species richness and diversity appear to be affected by slight differences in size and amounts of surface rock. High species richness and diversity were linked directly to intermediate levels of spatial

heterogeneity, defined by moderate habitat structure representing ecotones. Outside of these transitional areas (ecotones), species diversity increased in more spatially complex environments whereas species richness increased in less spatially complex environments. Intermediate levels of shrub abundance at the landscape level defined high levels of species richness and diversity whereas intermediate levels of grass abundance and medium sized rocks defined high levels of species diversity. These larger scale patterns of species richness and diversity added to the understanding of smaller scale patterns of species richness and diversity at Black Mesa.

Lastly, the production of vegetation and geologic maps demonstrated that the underlying spatial pattern of the geologic substrate was reflected in the broad patterns of vegetation. Additionally, surface geology, defined by rock cover and rock size better explained patterns of woody vegetation patterns at Black Mesa.

Keywords: Spatial heterogeneity, species richness and diversity, scale, natural fragmentation, habitat structure, heterogeneity hypothesis, TWINSPAN, detrended correspondence analysis, Oklahoma

Nomenclature: Flora of the Great Plains (Great Plains Flora Association 1986).

Introduction

Spatial heterogeneity is considered by several authors to be the single most important factor regulating the distribution of species (Wiens 1976; Tilman 1982; Urban et al. 1987; Huston 1994; Pollock et al. 1998). Spatial heterogeneity is defined as the degree of dissimilarity over a given aerial extent (Risser 1987). As spatial heterogeneity increases, so does species richness and diversity to a certain level (Forman and Godron 1986; Malanson 1993; Mourelle and Ezcurra 1997; Gould and Walker 1997; Von Numers and Van der Maarel 1998; Gould and Walker 1999). In more general terms, areas with a high degree of spatial heterogeneity tend to be more species rich and diverse (Grace and Pugesek 1997; Rosenzweig and Ambramsky 1997; Tilman 1997). Research involving spatial heterogeneity provides ecologists and biogeographers the opportunity to study the relationships between the organization of the physical landscape and species composition, richness and diversity.

Geomorphic and topographic factors play an important role in creating spatially complex landscapes and regulating species composition, richness and diversity (Whittaker 1956; Hack and Goodlett 1960; Ward et al. 1993; Wondzell et al. 1996; Bridge and Johnson 2000). These factors increase landscape heterogeneity and promote natural habitat fragmentation (Forman and Godron 1986). Fragmentation, a product of natural processes and anthropogenic activities, produces a landscape mosaic of interacting patches or polygons on a map coverage (Risser 1987; Turner 1989; Forman 1995). Consequently, landscapes with more diverse habitat structure, combined with an unequal distribution and flow of resources, tend to contain greater species richness and

diversity (Tilman 1982; Forman and Godron 1986; Schluter and Ricklefs 1993). Few studies involving landscape heterogeneity have focused on natural fragmentation and its influence on species composition, richness and diversity.

Studies involving heterogeneous landscapes have focused on patterns of vegetation distribution and species richness and diversity in relation to various biotic and abiotic factors at various scales. In the southern High Plains of North America, Hoagland and Collins (1997) showed that fine scale heterogeneity in playa lakes added to the regional heterogeneity and species richness. In a coastal marsh in northern Gulf of Mexico, Grace and Pugesek (1997) demonstrated that soil salinity, soil fertility and elevation were highly correlated with species richness. They also predicted an increase in species richness as within-plot heterogeneity increased. In studies by Hsieh et al. (1998), Vázquez and Givnish (1998) and Ward et al. (1993), altitudinal gradients played a dominant role in determining the distribution of species. Hsieh et al. (1998) and Vázquez and Givnish (1998) found that species richness and diversity decreased with an increase in altitude while Ward et al. (1993) showed an increase in species richness with altitude.

The interaction between landforms, geomorphic processes and soils often determine the distribution of plant communities. For example, underlying geology and landform type determine changes in vegetation composition in the northern Chihuahuan Desert (Wondzell et al. 1996) and species richness and diversity in Sonoran Desert bajadas (McAuliffe 1994). McAuliffe (1994) also noted that the highest species diversity was encountered on extremely unstable slopes, decreasing the amount of woody species and competitive exclusion. In

the Venezuelan Andes, the distribution of vegetation on talus slopes was correlated with large, coarse debris because it created a more stable environment for plant establishment (Pérez 1994). Finally, the gradients of slope angle, aspect, geologic substrate and nutrient availability best explained the distribution and richness of vegetation in Organ Pipe Cactus National Monument in the northern Sonoran Desert (Parker 1991).

These studies, and others, have focused on the effect of the environment on species distribution and/or species richness and diversity at one scale. Research involving species richness and diversity related to spatial heterogeneity at various scales is lacking. Studying differences in species richness and diversity at a landscape (regional) and sub-landscape (sub-regional) level provides a more accurate approach to measure and monitor patterns and change in biodiversity (Malanson 1993). Gould and Walker (1997) measured landscape scale variation in species richness along the length of the Hood River in the Northwest Territories of Canada. They also measured environmental variables that were important controls on species richness at scales from the site to the regional level. They discovered that regional species richness increased downstream and most of the variation in site richness along the river correlated with local environmental heterogeneity. Using the same data, Gould and Walker (1999) later discovered that species richness correlated with an increase in the number of communities. Differences in composition between communities were controlled the most by soil moisture and soil pH. In the Jornada del Muerto Basin in south-central New Mexico, Cornelius et al. (1991) demonstrated that species diversity was associated with geomorphological features at the landscape level,

especially landform type, but at the site level, species diversity was associated with available nitrogen and water.

The intermediate disturbance hypothesis (IDH) has been used in several studies to explain patterns of species richness and diversity. The IDH predicts that species richness or diversity is maximized by intermediate levels of environmental disturbance or stress (Grime 1973; Connell 1978; Huston 1979). It was first applied to herbaceous communities (Grime 1973; Al-Mufti 1977) and marine environments (Ward and Stanford 1983; Wilson and Keddy 1988; Gough et al. 1994) where the greatest species richness and diversity were measured at intermediate levels of biomass, a surrogate for productivity. For instance, Wilson and Keddy (1988) examined survivorship and growth of species along a wave action gradient at Axe Lake, Ontario, Canada. Species richness was greatest at intermediate levels of exposure to wave action and standing crop. More recently, the IDH concept has become an important component of research relating species richness and diversity to spatial heterogeneity and habitat structure (Noy-Meir 1985; Montaña 1990; Gould and Walker 1997). Literature in shoreline gradients (Wilson and Keddy 1988; Wisheu and Keddy. 1989) and dry environments (Montaña 1990; Valverde et al. 1996) suggest that species richness and diversity adhere to variations on the IDH at different scales.

This research focuses on landscape level patterns in a semi-arid environment, which consists of mesas and canyons in northwest Oklahoma. Among the state's most botanically unique and topographically complex areas, Black Mesa lies at a crossroads of four major biomes that contribute to the local species richness and diversity. The main goal of this research is to evaluate the

effect of spatial heterogeneity at the landscape and sub-landscape scales on the distribution of vegetation at Black Mesa, a spatially complex and naturally fragmented landform. More specifically, this study will focus on how species richness and diversity and its pattern are related to vegetation composition, geomorphology and topography, and landscape structure at the landscape and sub-landscape scales. It is hoped that the results of this research will add to a growing body of literature, which focuses on how species richness and diversity respond to different levels of spatial heterogeneity at different scales.

Study area

This study encompasses an area of about 18 sq km and includes Black Mesa and its surrounding landscape. Black Mesa is located in the far northwest corner of Cimarron County, Oklahoma, and is the eastern most extension of Mesa de Maya, a lava-capped plateau approximately 72 km in length and 600 m to 10 km wide (Rothrock 1925) (Figure 1). The study area contains the 648 hectares denoted as Black Mesa Nature Preserve, which is jointly administered by the Oklahoma State Park System and The Nature Conservancy. The remaining 1152 hectares (64% of the study area) is in private ownership.

The Mesa de Maya has long been recognized as a biogeographically unique region on the Great Plains. In Oklahoma, the eastern most extension of the Rocky Mountain Foothills meets portions of the western most extension of the Eastern Deciduous Forest. Mixed into these two biomes is the vegetation of the Great Plains and the Desert Southwest (Rogers 1949). The diversity of vegetation at Black Mea results from complex spatial patterning from a combination of geomorphic and topographic factors. Thirty-one state rare species (23 plants and 8 animals) are found at Black Mesa (The Nature Conservancy 1998).

Climate

The climate of Black Mesa is semiarid and continental. The average annual precipitation in Kenton (2 miles south of Black Mesa) is 43.5 cm with most occurring during the spring and summer months (Schoff 1943; Murphy et al. 1956). The average annual mean temperature at Kenton is 12.2°C. The months

of July (25.1°C average) and August (24.1°C average) are the warmest while December (1.1°C average) and January (0.9°C average) are the coldest (Schoff 1943). On average, there are only four days a year when the temperature dips below -17.8°C and cold spells are short in duration. Temperatures of over 32.2°C normally occur about 60 days a year, but the heat is seldom oppressive because of the elevation and the low humidity (Murphy et al. 1956). Moisture stress is exacerbated by daily windy conditions with maximum velocities occurring in the afternoon and subsiding during the evening. In the winter, dry winds from the Rocky Mountains blow across Black Mesa while potential moisture from the Gulf of Mexico arrives during the spring, summer and early fall (Schoff 1943; Murphy et al. 1956).

Geology

Black Mesa averages 168 meters of relief with an average elevation of 1494 meters on top and 1326 meters at the base. Mesa de Maya, including Black Mesa, is an example of inverted topography that represents 250 million years of visible geologic history (Suneson and Luza 1999). It consists of layered deposits of sandstone, shale, clay and limestone. These sedimentary deposits are capped by a resistant layer of dark brown and black basalt, giving Black Mesa its name (Rogers 1949). The near-vertical slopes below the lava cap are littered with angular basalt talus fragments while sandstone and shale slopes are littered with large sandstone blocks. The source of this Late Tertiary basalt is from Piney Mountain, an extinct volcano, which flowed two to five million years ago (Rothrock 1925). The geologic stratigraphy of Black Mesa, from higher to

lower elevation consists of: Raton Basalt (Tb), Ogallala Formation (To), Dakota Formation (Kd), Purgatoire Formation (Kp) and the Morrison Formation (Jm) (Figure 2).

The Raton Basalt increases in thickness from approximately 15 meters (m) to about 26 m at the New Mexico/ Oklahoma border. The Ogallala Formation is a moderately permeable mixture of braided stream deposits containing sand, silt, clay, gravel and limy sediments (Schoff 1943; Stovall 1943). The bulk of the formation is composed of fine-grained, well-sorted sand that varies in thickness from 23m to 61m (Rothrock 1925). The Dakota Formation is composed of lower sandstone, middle shale and upper sandstone members (Schoff 1943; Stovall 1943). The lower sandstone member of the Kd is the upper of two massive sandstone beds that are prominent features of Mesa de Maya (the lower of the two massive sandstone beds is part of the Kp). It also is the caprock of adjacent mesas and buttes (Rothrock 1925). The maximum height of the Kd is 56 m (Stovall 1943).

The Purgatoire Formation consists of the Kiowa shale overlying the Cheyenne sandstone and ranges in thickness from approximately 12 m to 36 m (Rothrock 1925; Stovall 1943). The Kiowa shale is a dark gray to black fossiliferous shale which grades into a sandy shale and platy sandstone (Rothrock 1925). The Cheyenne sandstone is the lower of two massive sandstone beds visible on Mesa de Maya. It is buff to white in color, course-grained and poorly structured (Rothrock 1925). The Morrison Formation is the most widespread formation with a maximum thickness of 142 m (Stovall 1943). It is found on the lower slopes and base of Black Mesa and is composed of

variegated shale, clay, marl, sandstone, conglomerate and limestone. Some dolomite and quartzite are also present (Schoff 1943).

Soils

Soils at Black Mesa are Entisols (Gray and Roozitalab 1976), which are mostly shallow and rocky, and occur on steep slopes. Surface soils (A horizon) have little organic matter accumulation and show little or no evidence of soil formation. Parent material occurs immediately below the A-horizon because clay or organic matter has been lost by eluviation. The major soil types at Black Mesa, from higher to lower elevation, are Apache (top), Rough stony land (mid-to-upper slopes), Travesilla (mid-to-lower slopes) and Berthoud (base) (Murphy et al. 1956; Gray and Roozitalab 1976).

Apache stony clay loam (Aa) varies from a few inches to several feet in depth and is found on the top of Black Mesa. These soils are composed mostly of clay from the weathering of basalt, along with scattered fragments of basalt (Rogers 1953, 1954; Gray and Galloway 1969). The soils that occupy the upper to mid slopes of Black Mesa are Rough stony land (Rf), which is a mixture of transported sand and gravel with a significant amount of clay derived from weathered basalt. The topography is a combination of talus, scattered rock fragments and steep sandstone escarpments. Rough stony land contains a very small amount of true soil since slopes range from about ten percent to nearly vertical cliffs. Upper slopes are scattered with basalt blocks with an increasing abundance of sandstone blocks further down slope (Murphy et al. 1956; Gray and Galloway 1969). Travesilla stony loam (Ta) and Berthoud loam soils (Bc)

are found on the lower slopes and flat areas below Rf soils and develop from loose colluvium from the upper slopes. Ta soils occur on 2 to 12 percent slopes and are relatively shallow. Bc soils are the deepest, most permeable and mature soils and occur on 3 to 5 percent slopes. In many places the Ta soils slope toward the non-stony, gentle foot slopes of the Bc soils (Murphy et al. 1956; Gray and Galloway 1969).

Vegetation

Rogers (1949) described four major vegetation types at Mesa de Maya: prairie, foothill, Rocky Mountain and riparian. Prairie vegetation occurs on mature soils with minimal erosion (Rogers 1953) and is dominated by Bouteloua gracilis and Bouteloua hirsuta. Bouteloua hirsuta is more abundant in sandier areas whereas Bouteloua gracilis is more plentiful throughout the study area (Bruner 1931; Blair and Hubbell 1938). In areas of greater water availability, Andropogon barbinodis, Andropogon gerardii, Andropogon saccaroides and Schizachyrium scoparium dominate.

Rocky Mountain and foothill vegetation is limited to canyons, talus and mesa slopes where erosion, deposition, accumulation of moisture, shading, slope and other environmental factors produce a variety of microhabitats (Rogers 1954). The dominant woody plants characteristic of these areas include: Celtis reticulata, Juniperus monosperma, Ptelea trifoliata, Rhus aromatica and Sapindus saponaria. Thick stands of woody vegetation grow near talus, drainage and canyon areas and are frequently interrupted by large basalt or sandstone blocks. Vegetation cover ranges from nearly impenetrable thickets,

especially on north facing slopes, to less dense woody vegetation interspersed with prairie vegetation on south facing slopes (Rogers 1954). Although no riparian vegetation was included in this study, Rogers (1949) showed that cottonwood and willow species dominated.

Methods

Data Collection

Vegetation data were collected from three permanent transects traversing Black Mesa. Each transect was spaced approximately one mile apart and oriented approximately perpendicular to contour lines. These transects were designated as east, central and west and were composed of 26, 26 and 21 quadrats respectively. Each quadrat measured 10 x 10 meters and was placed at 75 meter intervals along the transect. In order to increase the sample size, five additional temporary transects totaling 28 quadrats were located on the slopes in spatially complex areas (Figure 3).

Quadrats along each permanent transect were sampled twice during the 1998 growing season from May through October and once in May (1999). Temporary transects were sampled once during the 1998 growing season. The first quadrat for slope transects was placed just below the rim of the Mesa and extended downward. Transects on the top began at the north rim and ended at the south rim. All species in the quadrat were recorded and percent cover (abundance) was visually estimated using the following scale: 1, 5, 10, 20, ... , 100.

Because rock fragments and boulders are an integral part of Black Mesa, percent rock cover for each plot was visually estimated within each quadrat. In addition, percent rock cover within seven predetermined rock size classes (S1: < 78 cm^2; S2: 78 - 235 cm^2; S3: 235 - 392 cm^2; S4: 392 - 785 cm^2; S5: 785 - 1570 cm^2; S6: 1570 - 2355 cm^2; S7: > 2355 cm^2) were visually estimated with the same scale. Maximum rooting depth (soil depth) was calculated using a 30 cm

steel spike. The spike was driven into the ground at three locations (NW, center, SE) in each quadrat and average depth calculated. Percent slope of each quadrat was determined using a Suunto clinometer and aspect using a Suunto compass adjusted for magnetic north. Elevation of each quadrat was determined using a Thommen® Digital Altronic Traveller® Altimeter. Universal Transverse Mercator (UTM) coordinates were obtained for each quadrat using a global positioning system.

Data Analysis

Two scales of resolution were used in this research. First, cover values were complied into a species-by-site matrix and analyzed using two-way indicator species analysis (TWINSPAN, Hill 1979) classification within PC-ORD (McCune and Mefford 1997). TWINSPAN is a polythetic divisive classification technique that combines all species into a single cluster and successfully divides the species into a hierarchy of smaller clusters (Gauch 1982). The results from TWINSPAN served as mapping units for the vegetation map, which was used in landscape level (regional) analysis. Second, four sub-landscape (sub-regional) vegetation maps (north facing slopes, south facing slopes, top and base of Black Mesa) were produced for a finer scale analysis of landscape structure and diversity. The four sub-regions represented an average of 101 quadrats from the entire landscape.

Species richness (S), evenness (E; Pielou 1977) and Shannon's diversity index (H'; Shannon and Weaver 1949) were calculated at each scale using PC-ORD (McCune and Mefford 1997). Species diversity is comprised of two

components, the number of species in a given area (species richness) and equitability of their abundance (species evenness) (Peet 1974; Magurran 1988). The Shannon index of diversity (H') has been the most widely used index in community ecology and is defined as $H' = - \Sigma p_i \ln p_i$ where H' describes the average degree of uncertainty of predicting the species of an individual picked at random from the area or habitat. This uncertainty increases both as the number of species increases and as the individuals are distributed more equitably among the species already present. The parameter p_i is the decimal fraction of individuals belonging to the ith species (Ludwig and Reynolds 1988; Cox 1996). The most common evenness index used by ecologists is $E = H' / \ln (S)$ and is similar to J' of Pielou (1977).

In addition, total mean grass cover (TMGC), total mean forb cover (TMFC), total mean shrub cover (TMSC) and total mean rock cover (TMRC) were also calculated for each scale. Using SPSS (1988), correlation matrices were produced to explore the relationships between the diversity measures (S, E and H'), vegetation composition variables (TMGC, TMFC, TMSC and TMRC) and geomorphic and topographic variables (soil depth [SD], slope [SL], elevation [EL] and seven rock sizes [classes S1-S7]) at each scale. Non-parametric statistics (spearman's rho correlation coefficient) were used since the data were not normal.

Vegetation associations were mapped on a scanned 36 X 36 inch 1990 aerial photograph of Black Mesa (1:10,000) using Arc/View™ and Arc/Info™ GIS (ESRI 1995). A USGS 1:24,000 topographic map (Kenton Quadrangle) was used to geo-reference the aerial photograph to a UTM coordinate system. The

resulting map was geo-rectified using ERDAS Imagine software (with an overall location error of 20 pixels or 20 feet). Photographs, quadrat location and field notes increased the accuracy of the digitizing process. From the final landscape level map, four sub-landscape level maps were produced. All maps were projected in the UTM coordinate system.

Using the same aerial base map and reference to photographs, field notes and the research of Rothrock (1925); Stovall (1943); Schoff (1943); Sapik and Goemaat (1973); Suneson and Luza (1999) and Furr (2000), geologic zones were digitized. Development of a digital geologic map followed the same procedure outlined for the vegetation map. In order to analyze the spatial relationship between geologic zones and vegetation associations, ArcView™ GIS was used.

Landscape structure was analyzed and quantified at both scales using FRAGSTATS, a spatial pattern analysis program (McGarigal and Marks 1994). FRAGSTATS quantifies the aerial extent and spatial distribution of patches within a specified landscape in terms of landscape structure indices or metrics (McGarigal and Marks 1994). Landscape metrics calculated were area (CA, class area; %LAND, percent landscape), density/size (NP, number of patches; MPS, mean patch size), edge (TE, total edge) and shape (FD, average weighted mean patch fractal dimension) (Table 1).

These metrics were used to analyze landscape structure because they were the best indicators of the relationship between landscape structure and species richness and diversity (Forman and Godron 1986). Using SPSS (1998), correlation matrices were produced to explore the relationships between diversity

measures (S, E and H') and landscape structure metrics at the landscape and sub-landscape scales. In addition, correlation matrices were produced to explore the relationships between landscape structure metrics, vegetation composition variables (TMGC, TMFC, TMSC and TMRC) and geomorphic and topographic variables (soil depth [SD], slope [SL], elevation [EL] and rock sizes [classes S1-S7]) at both scales. Non-parametric statistics (spearman's rho correlation coefficient) were used since the data were not normal.

In addition to correlating spatial heterogeneity (defined by mean totals of vegetation composition variables, geomorphology and topographic variables and landscape structure metrics) with species richness and diversity, curvilinear relationships between spatial heterogeneity and species richness and diversity were analyzed in reference to the intermediate disturbance hypothesis at the landscape level. Sub-landscape patterns were not included because the sample size (4) was too small to determine any pattern.

Results

Vegetation Classification

In this study, 101 quadrats were sampled and 159 species encountered. Of these, 35 were grass species, 106 were forb species and 18 were woody species. The number of species per quadrat ranged from 10 to 50 with an average of 28 species per quadrat. Species with the highest relative frequency were Opuntia phaeacantha (94%), Opuntia imbricaria (87%), Bouteloua curtipendula (83%) and Bouteloua gracilis (82%). Average species cover per quadrat ranged from 0.01 to 16 percent cover, Bouteloua gracilis (16.3%) and Bouteloua curtipendula (11%) representing the highest average cover.

Nine vegetation associations were recognized, based upon the results of the TWINSPAN classification. The nine vegetation associations, along with species frequencies and mean cover values, are listed in Appendix I. The nine vegetation associations were grouped into herbaceous, shrubland and woodland subtypes (Figure 4). The herbaceous subtypes consisted of five associations dominated by Bouteloua gracilis, Bouteloua hirsuta and/or Bouteloua curtipendula. Herbaceous associations were found on the top, bottom and mid to lower slopes of Black Mesa. Shrubland subtypes contained three associations dominated by Rhus aromatica, Juniperus monosperma , Andropogon geradii, and Bouteloua curtipendula. These associations were found on upper slopes, talus cones, drainages and canyons. The woodland category consisted of one association dominated by Juniperus monosperma and was mostly found near drainages and on the mid to lower elevation north facing slopes. A more detailed description of the nine associations is presented in Appendix II.

Landscape level Analysis.

Landscape Structure and Species Richness and Diversity

Collectively, herbaceous associations comprised 86% of the landscape (1,653 hectares) while the woody associations comprised the remaining 14% of the landscape (272 hectares). The herbaceous associations contained a total of 46 patches with a mean patch size of 68 hectares. Conversely, the woody associations contained a total of 56 total patches with a mean patch size of 7 hectares. The difference between the herbaceous associations and woody associations in fractal dimension was small, 1.38 and 1.41, respectively.

Between associations, A4 occupied almost 40% of the landscape (760 ha) and had the largest patch average (190 ha). Conversely, A6 comprised only 1% of the total landscape (23 ha) and had the smallest patch average (3 ha). A9 had the most patches (34) while A1 and A8 contained the least number of patches (3). A8 had the largest fractal dimension (1.47), followed by A2, A5 and A7 (1.45). The lowest fractal dimension was recorded for A1 (1.31), on the top of Black Mesa.

Correlation results between diversity measures and landscape structure metrics did not reveal any significant relationships at the landscape level. One weak positive relationship existed between species richness and total edge (r^2=0.47, $p<0.05$). Additionally, correlation results between vegetation composition variables, geomorphic and topographic variables and landscape metrics were not significant.

Geomorphology, Topography and Species Richness and Diversity

Figure 5 shows the distribution of the five geologic zones. The Morrison covered the greatest area (59%), followed by Raton (22%), Dakota (10%), Purgatoire (6%) and Ogallala (3%). By overlaying the vegetation and geology maps, each vegetation association included an average of 70 percent of one geologic zone. More specifically, each vegetation association corresponded to an average of 88 percent of one geologic zone whereas each woody association corresponded to only 52 percent of one geologic zone.

The deepest soils were associated with the top (A1), base (A4) and mid-to-lower north facing slopes (A5). The shallow soils occurred in drainages (A9), canyons (A6) and upper south facing slopes (A8). The steepest slopes occurred on the upper north facing (A7) and south facing (A8) slopes, while the gentlest slopes occurred on the top (A1) and near the edge (A2). Small rock classes were most frequent on top (A1) and near the edge (A2) and least frequent in the canyons (A6). The largest rock classes were the most frequent in canyons (A6) and the upper north facing (A7) and south facing slopes (A8) but were infrequent on the top (A1). In general, the mid-sized rock classes occurred most frequently on the mid to upper slopes and least often on the top.

There were no statistically significant relationships between diversity measures and geomorphic and topographic variables at the landscape level. On the other hand, relationships among the geomorphic and topographic variables were noteworthy. Greater soil depths were directly related to the smallest rock class (S1; r^2=0.61, $p<0.05$) and inversely related to the largest rock class (S7; r^2=-0.52, $p<0.05$) and rock cover (r^2=-0.56, $p<0.05$). Slope was directly related to

the largest rock class (S7; r^2=0.76, $p<0.05$) and rock cover (r^2=0.81, $p<0.05$) and inversely related to smaller rock classes (S1; r^2=-0.72, $p<0.01$; S2; r^2=-0.52, $p<0.05$).

Vegetation composition and species richness and diversity

Comparing herbaceous (H) and woody (W) associations, herbaceous associations were higher in grass (H: 61%; W: 35%) and forb (H: 19%; W: 10%) cover while the woody associations were higher in shrub (H: 6%; W: 31%) and rock cover (H: 14%; W: 24%). Based on individual associations, the highest species richness occurred in A9, a moderately wooded association, followed by herbaceous associations A2 and A3. The highest species diversity values were found in moderately woody associations (A8 and A9) and mid-elevation mixed grassland on north facing slopes (A5) (Table 2). Conversely, the lowest species richness occurred in densely wooded shrublands (A6, A7) while the lowest species diversity occurred in the densely wooded associations (A6, A7) and the grassland association on the top (A1).

Correlation results did not reveal any significant relationships between diversity measures and vegetation composition variables at the landscape level. On the other hand, some relationships among the vegetation composition variables were noteworthy. Total mean shrub cover was positively correlated with total mean rock cover (r^2=0.47, $p<0.05$) and negatively correlated with total mean grass cover (r^2=-0.90, $p<0.05$) and total mean forb cover (r^2=-0.93, $p<0.05$). Also, total mean grass cover was positively correlated with total mean

forb cover (r^2=0.84, $p<0.05$) and negatively correlated with total mean rock cover (r^2=-0.44, $p< 0.05$).

At the landscape level, species richness and diversity displayed several curvilinear (unimodal) relationships. Species richness (r^2=0.68, $p<0.05$) and diversity (r^2=0.86, $p<0.05$) were greatest at intermediate levels of shrub cover, a measure of abundance (Figure 6a). High levels of species richness and diversity occurred around 20% and 30% shrub cover, respectively. Species diversity was also greater at intermediate levels of grass cover (r^2=0.84, $p<0.05$) and medium to large rock sizes (S5; r^2=0.89, $p<0.05$) (Figure 6b). High levels of species diversity occurred around 60% grass cover, which demonstrated that high species diversity occurred in environments with approximately 60% grass cover and 20% shrub cover. Additionally, an area with 10% medium sized rocks also defined environments with high species diversity. The results also showed that 3% medium sized rocks corresponded to areas with little topography (low species diversity) and an area with 17% medium sized rocks corresponded to areas with the largest sized rocks, steepest slopes and greatest rock cover (low species diversity).

Sub-landscape level Analysis

Landscape Structure and Species Richness and Diversity

The bottom comprised the majority of the landscape (48%) (924 ha) and contained the lowest fractal dimension (1.33). The north facing slopes comprised the smallest portion of the landscape (14%) (271 ha) and had the highest fractal dimension (1.4). It also had the smallest mean patch size (6 ha), the most

patches (47) and the largest total edge (33,147 m). The top had the least number of patches (2), the largest mean patch size (211 ha) and the smallest total edge (17,112 m).

Correlation results between diversity measures and landscape structure metrics revealed several significant relationships at the sub-landscape level. Species richness was negatively correlated with percent landscape (%LAND; r^2=-0.64, $p<0.05$) and class area (CA; r^2=-0.64, $p<0.05$). Species diversity was positively correlated with number of patches (NP; r^2=0.64, $p<0.05$) and total edge (TE; r^2=0.64, $p<0.05$) and negatively correlated with mean patch size (MPS; r^2=-0.64, $p<0.05$).

Correlation results between vegetation composition variables and landscape metrics were also significant. Shrub cover was directly related to number of patches (NP; r^2=0.89, $p<0.05$) and total edge (TE; r^2=0.82, $p<0.05$) and inversely related to class area (CA; r^2=-0.64, $p<0.05$), percent landscape (%LAND; r^2=-0.64, $p<0.05$) and mean patch size (MPS; r^2=-0.84, $p<0.05$). Grass cover was directly related to class area (CA; r^2=0.64, $p<0.05$), percent landscape (%LAND; r^2=0.64, $p<0.05$) and mean patch size (MPS; r^2=0.82, $p<0.05$) and inversely related to number of patches (NP; r^2=-0.89, $p<0.05$) and total edge (TE; r^2=-0.84, $p<0.05$). Rock cover was directly related to number of patches (NP; r^2=0.64, $p<0.05$) and total edge (TE; r^2=0.64, $p<0.05$) and inversely related to mean patch size (MPS; r^2=-0.64, $p<0.05$). Forb cover directly related to mean patch size (MPS; r^2=0.64, $p<0.05$) and inversely related to number of patches (NP; r^2=-0.64, $p<0.01$) and total edge (TE; r^2=-0.64, $p<0.05$).

Correlation results between geomorphic and topographic variables and landscape metrics revealed three noteworthy relationships. The largest rock class (S7) was directly related to number of patches (NP; r^2=0.97, $p<0.05$) and total edge (TE; r^2=0.95, $p<0.05$) and inversely related to mean patch size (MPS; r^2=-0.84, $p<0.05$). The small rock class (S2) was directly related to mean patch size (MPS; r^2=0.99, $p<0.05$) and inversely related to number of patches (NP; r^2=-0.84, $p<0.05$) and total edge (TE; r^2=-0.85, $p<0.05$).

Geomorphology, Topography and Species Richness and Diversity

The south facing slopes contained slightly greater percent slopes and rock cover and slightly lower soil depths and percentage of smaller rocks when compared with the north facing slopes. The north facing slopes contained a slightly higher percentage of larger rocks when compared with the south facing slopes. Soil depths were slightly greater on top of the mesa when compared with the bottom. The top also had the lowest percentage of large rocks and rock cover while the bottom contained the highest percentage of small rock sizes.

Correlation results reveal many significant relationships between diversity measures and geomorphic and topographic variables at the sub-landscape level. Species richness was positively correlated with mid-sized rock classes (S4; r^2=0.97, $p<0.05$, S5; r^2=0.66, $p<0.05$) and negatively correlated with the smallest rock class (S1; r^2=-0.64, $p<0.05$). Species diversity increased with an increase in slope (r^2=0.98, $p<0.05$), rock cover (r^2=0.91, $p<0.05$) and larger rock classes (S5; r^2=0.66, $p<0.05$, S6; r^2=0.93, $p<0.05$, S7; r^2=0.87, $p<0.05$). Species diversity also increased with a decrease in soil depth (r^2=-0.98, $p<0.05$) and small rock

classes (S1; r^2=-0.97, $p<0.05$, S2; r^2=-0.64, $p<0.05$). Relationships among the geomorphic and topographic variables were similar to those found at the landscape level.

Vegetation composition and species richness and diversity

North facing slopes had the highest shrub cover and the lowest grass and forb cover and the south facing slopes had the greatest rock cover (Figure 7). The top also had the lowest shrub and rock cover and the highest grass and forb cover. Although two additional vegetation associations were found on the north facing slopes, the south facing slopes had higher species richness and diversity values (Figure 8). The mesa bottom had the lowest species richness and the top had the lowest species diversity. Unlike the landscape level, the correlation results between diversity measures and vegetation composition show many significant relationships. Species richness was positively correlated with TMRC (r^2=0.64, $p<0.05$) and species diversity was positively correlated with TMSC (r^2=0.66, $p<0.05$) and TMRC (r^2=96, $p<0.05$). Species diversity was negatively correlated with TMGC (r^2=-0.68, $p<0.05$). The relationships between the vegetation composition variables revealed the same significant relationships as in the landscape level.

Discussion

The relationships between vegetation composition, geomorphology and topography and landscape structure were similar at all spatial scales analyzed. This shows that the effect of spatial heterogeneity is consistent at both scales and provides a confident measure of significance between species richness and diversity and scale. It was shown that the effect of spatial heterogeneity at the sub-landscape scale had the most impact on species richness and diversity at Black Mesa.

Increased spatial heterogeneity and habitat fragmentation were defined by an increase in the number of patches and total edge and smaller patch sizes related to vegetation associations within each sub-region. Increased slope, rock cover and medium to large rocks, which proved to be major factors increasing species richness and diversity, dictated the degree of spatial heterogeneity and fragmentation. These results are consistent with other studies demonstrating the effects of surface rock cover on species richness and diversity explained by increased spatial heterogeneity and habitat structure.

For example, Montaña (1990) showed that the greatest species richness and diversity in the southern Chihuahuan Desert was linked to moderate habitat structure defined by rockiness, topography and soil texture. Similarly, Valverde et al. (1996) showed that species richness in the southern Chihuahuan Desert was correlated with landform type, a measure of landscape heterogeneity. High species richness and diversity related to surface rock cover and habitat structure was also reported in the Sonoran Desert and the Monte region in Argentina (Barbour and Diaz 1973) and the Negev Desert of Israel (Ward et al. 1993).

Additionally, Noy-Meir (1985) indicated that high species richness correlated with habitat structure (i.e. vertical and horizontal heterogeneity) and was defined by rocky surfaces and coarse-grained soils. This pattern also appeared in other environments as well. Shmida and Wilson (1985) detailed many studies where habitat structure and species richness were positively correlated. Gould and Walker (1997) also demonstrated that species richness along the Hood River in Northwest Territories of Canada was correlated with increasing environmental heterogeneity, defined from a suite of topographic, edaphic (soil-related) and geomorphic variables.

A mosaic of patches defined a substantial portion of the spatial heterogeneity at Black Mesa, which was a direct result of the dissected terrain littered with varying sizes and amounts of rock. Species richness and diversity appeared to be affected by slight differences in size and amounts of rock, as demonstrated by north and south facing slopes. Although the north facing slopes had a greater number of patches, the south facing slopes had greater species richness and diversity, which was a direct result of the slight differences in rock size and rock cover favoring south facing slopes. This seemed contradictory since species richness and diversity were directly related to larger rocks and rock cover (dominated by south facing slopes) and patchiness (north facing slopes). A possible explanation for increased species richness and diversity on south facing slopes was represented by the largest difference between the two sub-regions, shrub cover (i.e. a measure of abundance and to some degree, biomass), which predominated on north facing slopes and linked to variations of the intermediate disturbance hypothesis.

Although the greatest effect of spatial heterogeneity on species richness and diversity occurred at the sub-landscape scale, data collected at the landscape level were important in understanding patterns of sub-regional species richness and diversity. First of all, patterns of species richness and diversity at Black Mesa revealed that the greatest species richness and diversity were directly linked to intermediate levels of spatial heterogeneity, defined by moderate habitat structure (Tilman and Pacala 1993; Schluter and Ricklefs 1993). These environments contained a mixture of shrubland and grassland species defined by moderate levels of rock, grass and shrub cover, medium-sized rocks and slope steepness.

Secondly, greater spatial heterogeneity (more patchy and fragmented environments) increased species diversity defined by steeper slopes, increased rock cover and larger sized rocks (i. e. areas dominated by Rhus aromatica with other woody species abundant). On the other hand, less spatially complex environments (less structured) with less shrub cover (i. e. areas dominated by Juniperus monosperma) were related to increases in species richness defined by milder slopes, decreased rock cover and smaller sized rocks. These environments contained more grassland species, which increased the number of forb species and increased overall species richness. Lastly, nearly impenetrable wooded environments solely dominated by Rhus aromatica, especially on the north facing slopes, contained the lowest species richness and diversity. These impenetrable environments were extremely spatially complex and contained excessive rock cover, rock sizes and slope steepness.

The relationships discussed above parallel research relating species richness and diversity to intermediate levels of biomass and the IDH (Grime 1973; Al-Mufti 1977; Huston 1979; Tilman 1982; Wilson and Keddy 1988; Wisheu and Keddy 1989). These ideas have transformed the intermediate disturbance hypothesis into a heterogeneity hypothesis (Rosenzweig and Abramsky 1993), where intermediate levels of spatial heterogeneity (i.e. moderate habitat structure) occurred at intermediate levels of abundance (i.e. productivity or biomass).

More specifically, increased productivity (increasing the supply rate of a limiting resource leading to increased biomass) leads to increased competitive exclusion (Hardin 1960) or diffuse competition (Whittaker 1972) and a decrease in species richness and diversity, whereas intermediate levels of biomass moderates competitive exclusion and produces species rich and diverse habitats (Grime 1973; Huston 1979; Tilman 1982, 1986). Similar to partial competitive exclusion by Rhus aromatica on the slopes of Black Mesa, McAuliffe (1994) demonstrated that the shrub, Larrea tridentata decreased species richness on bajadas in the northeastern part of the Sonoran Desert and increased species diversity defined by higher rock cover, larger rock sizes and coarser-textured soils.

Higher species richness and diversity at intermediate levels of spatial heterogeneity and habitat structure were supported by several landscape level curvilinear relationships (Figures 6a and 6b). Intermediate levels of shrub cover defined peak levels of both species richness and diversity. Although the curves were not strictly concave down, they still showed that at low levels of shrub

cover, species richness and diversity levels were moderate and at high levels of shrub cover (i.e. north facing slopes), species richness and diversity were low. In addition, intermediate levels of grass cover and medium sized rocks defined high species diversity. When compared with the curve for shrub cover, three times as much grass cover defined areas of high species diversity. The combination of shrub and grass cover indicated a higher probability of increased species diversity rather than species richness, especially on south facing slopes where the interaction between grassland and shrubland species is the greatest. These environments represented ecotones, or transition zones (Forman and Moore 1992; Wiens 1992), defined by two vegetation associations, A3 and A9 (Figure 4).

The relationship between ecotones and high richness and diversity levels has been demonstrated in several studies. Whittaker and Niering (1965) showed that the greatest species diversity did not occur in the most productive, closed forests communities of the Santa Catalina Mountains in Arizona, but in less productive, open communities of intermediate composition among grasslands, shrublands and woodlands. Likewise, Peet (1978) showed that species diversity was greater in the grassland-forest ecotone in the Colorado Rocky Mountains. Gould and Walker (1997) demonstrated that the highest species diversity occurred at an ecotone where the Hood River in Northwest Territories of Canada begins to flow through uplifted sediments. Shmida and Wilson (1985) discovered floristic transition zones in the Judean Desert with high species richness.

Although this current study showed that species richness and diversity increased in transitional environments, it is not always the case. Lloyd et al.

(2000) demonstrated that ecotones have shown both increases and decreases in species diversity, and that general patterns depend more on ecological site conditions and species interactions. This is often related to the subjectivity of identifying ecotones and the scale of the ecotone (Gosz 1992). According to Gosz (1993), the most important processes affecting ecotones is related to scale. For instance, biome level ecotones are most affected by climate and topography whereas ecotones at finer scales are most affected by soil characteristics, inter- and intra-species interactions, microclimate and microtopography. Similarly, small scale patterns of species richness relate to factors that act on the small scale and are variable on the small scale and regional patterns of richness relate to factors showing large-scale variation (Currie 1991).

As mentioned earlier, there were many significant relationships relating vegetation composition, geomorphology, topography and landscape structure to species richness and diversity at the sub-landscape scale. Although there were no significant relationships at the landscape scale, it was shown that results from larger scale (landscape) patterns of species richness and diversity were important in understanding smaller scale (sub-landscape) patterns of species richness and diversity at Black Mesa. Similarly, regional species richness and diversity can be a very good predictor of, as well as influence, local species richness and diversity (Ricklefs 1987; Ricklefs and Schluter 1993; Caley and Schluter 1997). In retrospect, smaller scale conditions that create high species diversity tend to replicate similar patterns at larger scales (Wisheu and Keddy 1996). Likewise, regional diversity levels are not strictly a result of regional

processes but of local processes influenced by environmental conditions that are regionally similar (Huston 1999).

It also appeared that vegetation communities in semi-arid environments, such as Black Mesa, paralleled the distribution of geologic substrate. Analysis of the vegetation and geologic maps showed the underlying spatial pattern of the geologic substrate was reflected in the broad patterns of vegetation and was consistent with many geomorphologically-based studies (Hack and Goodlett 1960; Wright and Mooney 1965; Rhodes 1980; Ward et al. 1993). For example, Ward et al. (1993) showed the importance of geologic substrate (presence of basalt, quartz alluvium, etc.) on vegetation patterns in a Negev Desert cirque. Likewise, Rhodes (1980) correlated vegetation distributions with geologic formations at the state level in Oklahoma, whereas Hack and Goodlet (1960) correlated forest communities with geologic substrate in the central Appalachian Mountains.

Not mentioned in these studies, surface geology, defined by rock cover and rock size explained woody vegetation patterns at Black Mesa. For example, most woody species were highly correlated with the distribution of surface rock cover and larger rock sizes, which were vertically, not horizontally distributed in drainages, canyons and talus slopes. Since the distribution of surface rock cover and woody vegetation was not entirely defined by the horizontal geologic substrate at Black Mesa, surface rock cover was important to the distribution of woody communities in semi-arid environments where moisture (based on evaporation rates) is a limiting resource (Noy-Meir 1973). Increased rock cover and larger rocks with coarser soils allow more water infiltration and more plant-

available soil moisture for woody species due to lower evaporative losses. For example, Yang and Lowe (1956) showed that more woody species of the Paloverde-Sahuaro vegetation type dominated areas with more surface rock cover found in steeper slopes in the Sonoran Desert. Similarly, Bowers and Lowe (1986) showed many woody species were specifically located on the upper bajadas in the Sonoran Desert, where coarser-textured soils increased water potential.

Conclusions

This research evaluated the effect of spatial heterogeneity at the landscape and sub-landscape scales on the distribution of vegetation at Black Mesa in Cimarron County, Oklahoma. It stressed how species richness and diversity and its pattern were related to vegetation composition, geomorphology and topography, and landscape structure at the landscape and sub-landscape scales. The research presented here demonstrated that the effect of spatial heterogeneity at the sub-landscape scale had the most impact on species richness and diversity. Increased spatial heterogeneity and habitat fragmentation at Black Mesa were defined by an increase in the number of patches, total edge and smaller patch sizes. Increased slope, rock cover and medium to large rocks, which proved to be major factors increasing species richness and diversity, dictated the degree of spatial heterogeneity and fragmentation.

It was also determined that species richness and diversity were affected by slight differences in size and amounts of surface rock. High species richness and diversity were linked directly to intermediate levels of spatial heterogeneity,

defined by moderate habitat structure representing ecotones. Outside of these transitional areas (ecotones), species diversity increased in more spatially complex environments whereas species richness increased in less spatially complex environments. Patterns of species richness and diversity at the sub-landscape scale were refined by four curvilinear relationships at the landscape scale. Intermediate levels of shrub abundance at the landscape level defined high levels of species richness and diversity and intermediate levels of grass abundance and medium sized rocks defined high levels of species diversity.

Lastly, the production of vegetation and geologic maps demonstrated that the underlying spatial pattern of the geologic substrate was reflected in the broad patterns of vegetation. Additionally, surface geology, defined by rock cover and rock size better explained patterns of woody vegetation patterns at Black Mesa.

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Legend Table 1

A detailed description of the landscape metrics calculated using FRAGSTATS, a spatial pattern analysis program (McGarigal and Marks 1994). The subscripts used in the table are as follows: i = 1, ..., m or m'patch types; j = 1, ..., n patches; k = 1, ..., m or m' patch types. The symbols used in the table are as follows: A = total landscape area (m^2); a_{ij} = area (m^2) of patch ij; p_{ij} = perimeter (m) of patch ij; e_{ik} = total length (m) of edge in landscape between patch types i and k; n_i = number of patches in the landscape of patch type i.

CA	Class Area	$CA = \sum_{j=1}^{n} aij(1/10{,}000)$	Hectares	CA >0; CA approaches 0 as the patch type becomes increasingly rare in the landscape.	CA equals the sum of the areas (m^2) of all patches of the corresponding patch type, divided by 10,000 (to convert to hectares).
%LAND	Percent Landscape	$((\sum_{j=1}^{n} aij)/A)100$	Percent	0 < %LAND ≤ 100; % LAND approaches 0 when the corresponding patch type becomes increasingly rare in the landscape. %LAND = 100 when the entire landscape is comprised of a single patch.	%LAND equals the sum of the areas (m^2) of all patches of the corresponding patch type, divided be total landscape area (m^2), multiplied by 100 (to convert to a percentage). It equals the percentage the landscape comprised of the corresponding patch type.
NP	Number of Patches	n_i	None	NP ≥ 1, without limit; NP = 1 when the landscape consists of a single patch.	NP equals the number of patches of the corresponding patch type.

MPS	Mean Patch Size	$((\sum_{j=1}^{n} aij)/n_i)(1/10{,}000)$	Hectares	MPS > 0, without limit; The range in MPS is limited by the grain and extent of the image and the minimum patch size.	MPS equals the sum of the areas (m^2) of all patches of the corresponding patch type, divided by the number of the same type, divided by 10,000.
TE	Total Edge	$\sum_{k=1}^{m'} e_{ik}$	Meters	TE ≥ 0, without limit; TE = 0 when there is no class edge in the landscape.	TE equals the sum of the lengths (m) of all edge segments involving the corresponding patch type.
FD	Fractal Dimension	$\sum_{j=1}^{n} [((2\ln pij)/(\ln aij)) \times (aij/\sum_{j=1}^{n} aij)]$	None	1≤ FD ≤ 2; A fractal dimension greater than 1 for a 2-D landscape mosaic indicates a departure from a Euclidean geometry (i.e. an increase in patch shape complexity). FD approaches 1 for shapes with very simple perimeters such as circles or squares, and approaches 2 for shapes with highly convoluted, plane-filling perimeters.	FD equals the sum, across all patches of the corresponding patch type, of 2 times the logarithm of patch perimeter (m) divided by the logarithm of patch area (m^2), multiplied by the patch area (m^2) divided by total class area (sum of patch area for each patch of the corresponding patch type).

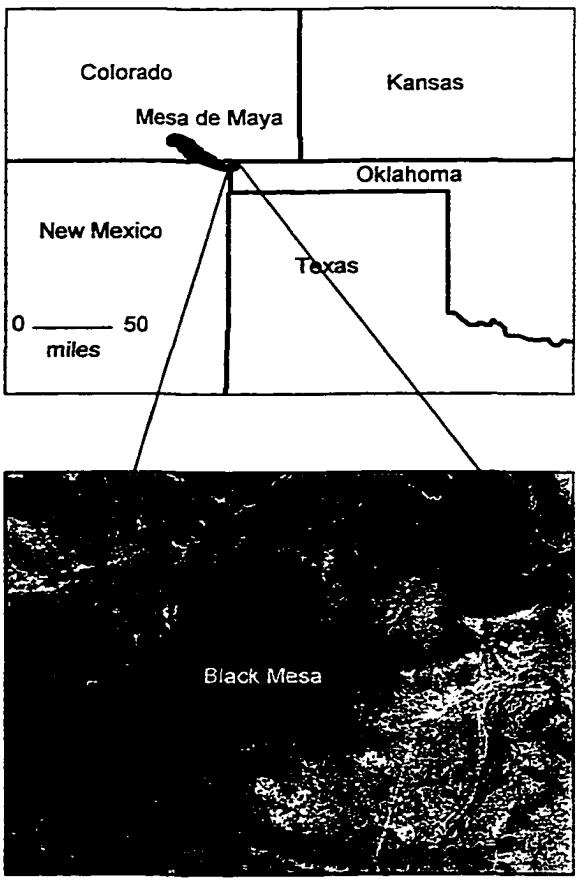
Legend Table 2

The relationship between vegetation associations (A1-A9) and diversity measures (S = species richness, E = species evenness (Pielou 1977) and H' = Shannon's diversity index (Shannon and Weaver 1949).

Associations	S	E	H'
A1	74	0.582	2.504
A2	99	0.689	3.165
A3	98	0.696	3.191
A4	90	0.7	3.152
A5	60	0.809	3.312
A6	61	0.685	2.817
A7	37	0.589	2.126
A8	93	0.761	3.448
A9	105	0.706	3.287
Average	80.33	0.69	3.02

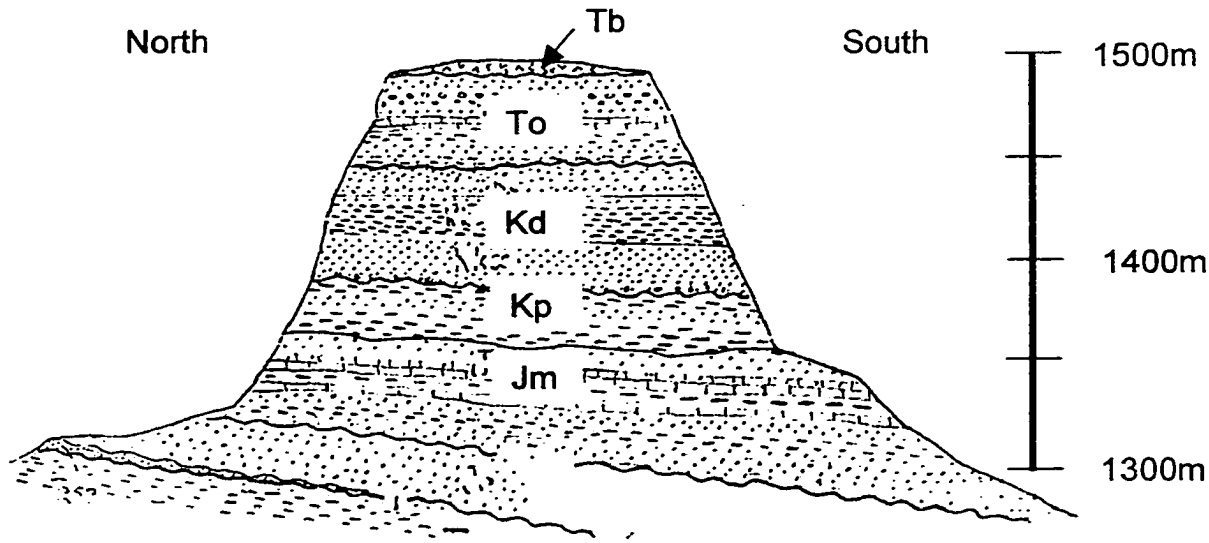
Legend Figure 1

Study Area. The Mesa de Maya is a lava-capped plateau approximately 72km in length and from 600 to 10km wide. It extends from southeastern Colorado through the northeastern corner of New Mexico and into the northwestern tip of the Oklahoma Panhandle. Most of the plateau lies in Colorado and New Mexico, where it is called Mesa de Maya, while the easternmost lobe, which extends 5 km into Cimarron County, Oklahoma, is known as Black Mesa. This study was conducted in an area of about 18 sq km and includes Black Mesa and its surrounding landscape.


Colorado
Kansas
Mesa de Maya
Oklahoma
New Mexico
Texas
0 ——— 50
miles
Black Mesa

Legend Figure 2

The geologic stratigraphy of Black Mesa, from higher to lower elevation consists of: Raton Basalt (Tb), Ogallala Formation (To), Dakota Formation (Kd), Purgatoire Formation (Kp) and the Morrison Formation (Jm)


North
Tb
South
1500m
To
Kd
1400m
Kp
Jm
1300m

Legend Figure 3

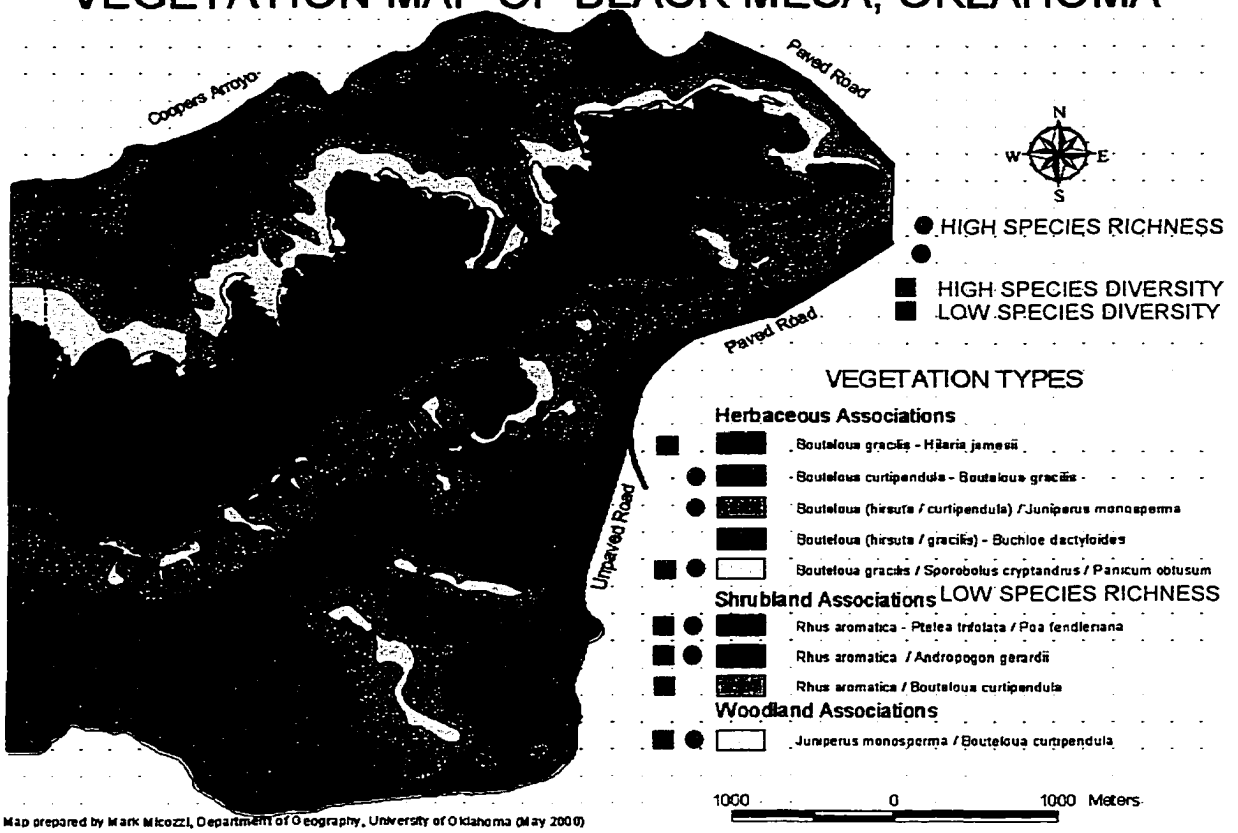
Location of permanent and temporary transects on a portion of the Kenton USGS 1:2400 Quadrangle. Vegetation data were collected from three permanent transects traversing Black Mesa. Each transect was spaced approximately one mile apart and oriented approximately perpendicular to contour lines. These transects were designated as east, central and west and were composed of 26, 26 and 21 quadrats respectively (blue lines). Each quadrat measured 10 x 10 meters and was placed at 75 meter intervals along the transect. In order to increase the sample size, five additional temporary transects totaling 28 quadrats were located on the slopes in spatially complex areas (short black lines).

K
Miles
0
1
N
Black Mesa
State Park
Oklahoma
Texas
Cimarron
Kenton
Boise City
Felt
Keyes
Hardesty
Optima
Guymon
Goodwell
Texhoma
Turpin
Hooker
Adams
Balko
Beaver
Forgan
Gate
Slapout
Knowles
Mocane
Laverne
Fargo
Gage
Arnett
Shattuck
Buffalo
Waynoka
Alva
Cleo Springs
Jet
Chapman
Ames
Canton
Watonga
Geary
Calumet
Mustang
Yukon
Piedmont
Guthrie
Edmond
Oklahoma City
Norman
Moore
Tuttle
Newcastle
Blanchard
Purcell
Lexington
Noble
Pauls Valley
Wayne
Elmore City
Davis
Sulphur
Ardmore
Marietta
Thackerville
Gene Autry
Tishomingo
Madill
Kingston
Durant
Caddo
Hugo
Boswell
Fort Towson
Idabel
Broken Bow
Antlers
Hochatown
Valliant
Wright City
Clayton
Tuskahoma
Talihina
Poteau
Heavener
Howe
Wister
Spiro
Sallisaw
Muldrow
Fort Smith
Van Buren
Alma
Mulberry
Ozark
Clarksville
Russellville
Dardanelle
Ola
Atoka
Tushka
Stringtown
Caney
Bokchito
Achille
Calera
Kemp
Colbert
Bennington
Willis
Bokchito
Hendrix
Durant
Caddo
Hugo
Boswell
Fort Towson
Idabel
Broken Bow
Antlers
Hochatown
Valliant
Wright City
Clayton
Tuskahoma
Talihina
Poteau
Heavener
Howe
Wister
Spiro
Sallisaw
Muldrow
Fort Smith
Van Buren
Alma
Mulberry
Ozark
Clarksville
Russellville
Dardanelle
Ola
Atoka
Tushka
Stringtown
Caney
Bokchito
Achille
Calera
Kemp
Colbert
Bennington
Willis
Bokchito
Hendrix

Legend Figure 4

Vegetation map showing the nine vegetation associations grouped into three subtypes: herbaceous, shrubland and woodland. Associations are in numerical order starting with A1 (Bouteloua gracilis – Hilaria jamesii) and ending with A9 (Juniperus monosperma / Bouteloua curtipendula). Also shown are levels of species richness and diversity for each association.

VEGETATION MAP OF BLACK MESA, OKLAHOMA

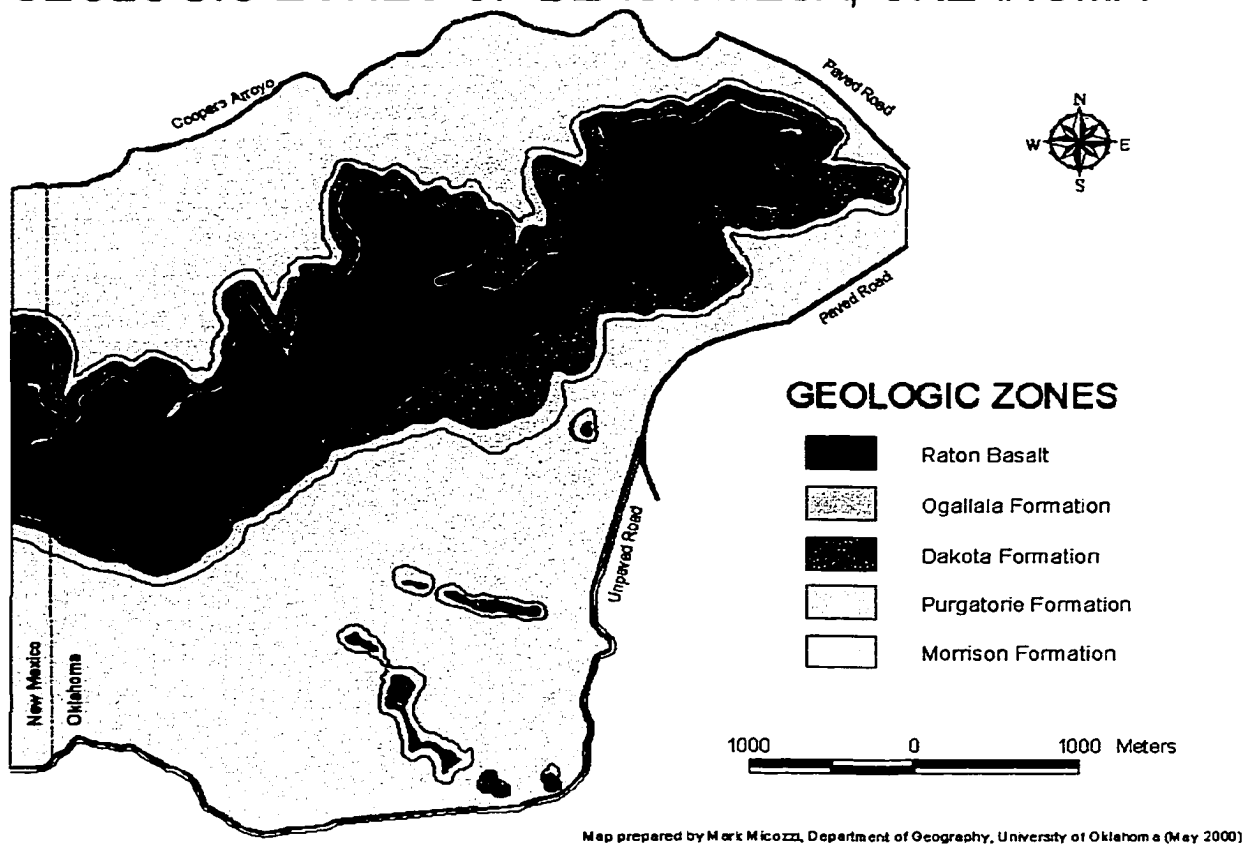


Map prepared by Mark Micozzi, Department of Geography, University of Oklahoma (May 2000)

Legend Figure 5

Geologic map of Black Mesa showing the five major geologic zones. The Morrison Formation covers the greatest area (59%), followed by Raton Basalt (22%), Dakota Formation (10%), Purgatoire Formation (6%) and Ogallala Formation (3%).

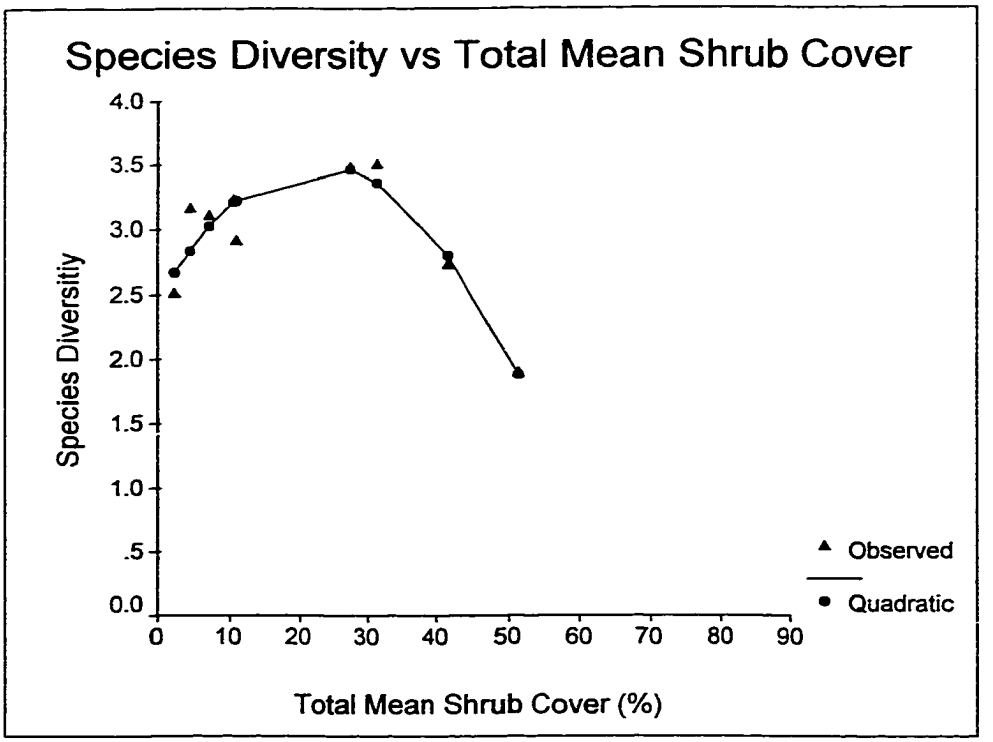
GEOLOGIC ZONES OF BLACK MESA, OKLAHOMA

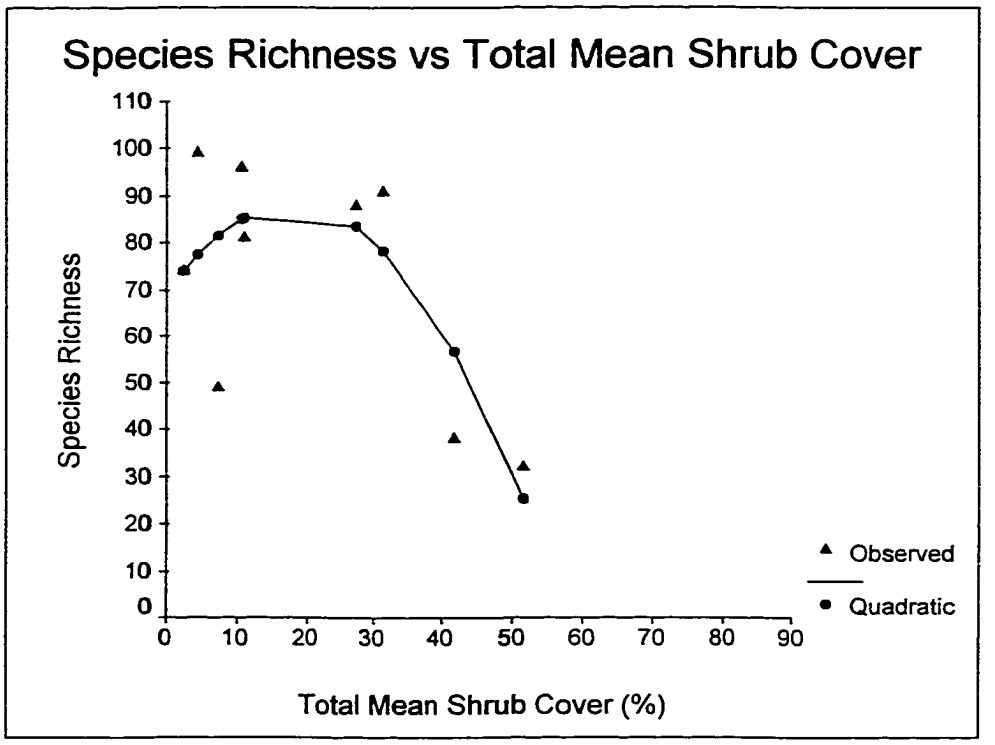


Map prepared by Mark Micozzi, Department of Geography, University of Oklahoma (May 2000)

Legend Figure 6a

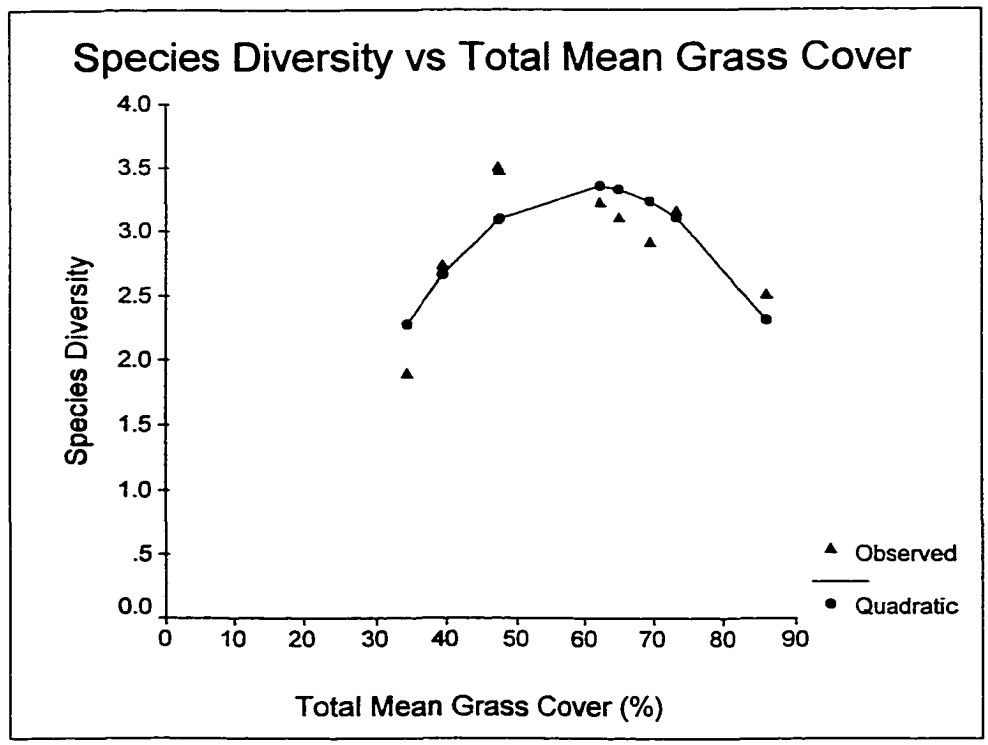
Curvilinear relationships at the landscape scale. Species richness (r^2=0.68, p=0.032) and species diversity (r^2=0.86, p=0.003) were greatest at intermediate levels of shrub cover. At low levels of shrub cover, species richness and diversity levels are moderate and at high levels of shrub cover, species richness and diversity are low. High levels of species richness and diversity occurred around 20% and 30% shrub cover, respectively.

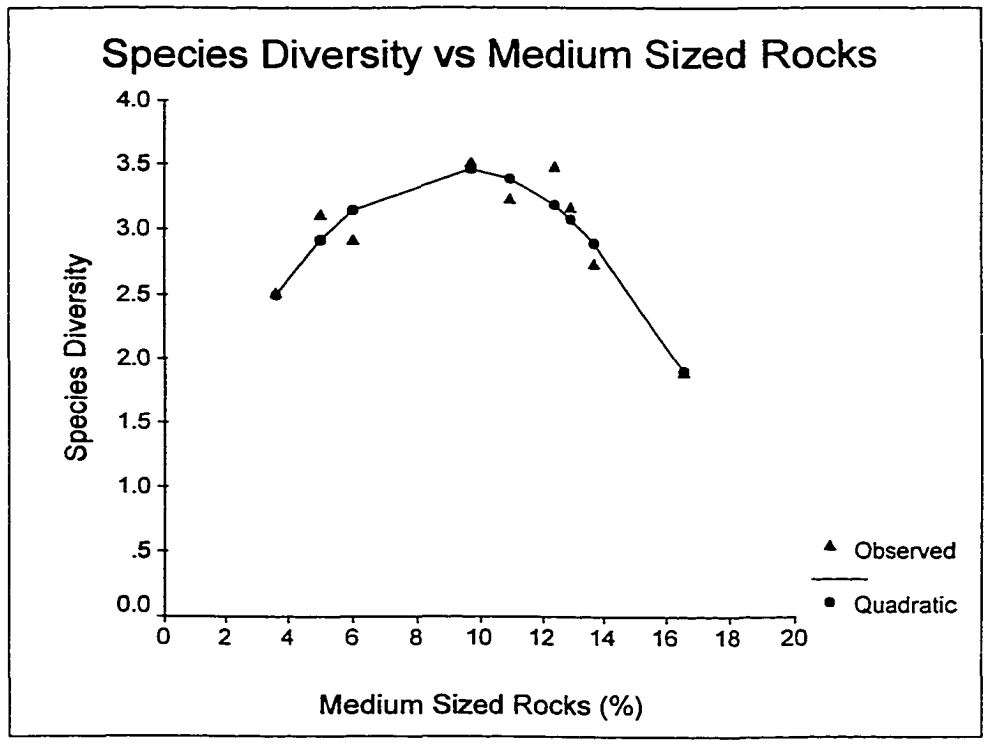

Species Diversity vs Total Mean Shrub Cover
Species Diversity
4.0
3.5
3.0
2.5
2.0
1.5
1.0
.5
0.0
0
10
20
30
40
50
60
70
80
90
Total Mean Shrub Cover (%)
Observed
Quadratic


Species Richness vs Total Mean Shrub Cover
Species Richness
110
100
90
80
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
80
90
Total Mean Shrub Cover (%)
Observed
Quadratic

Legend Figure 6b

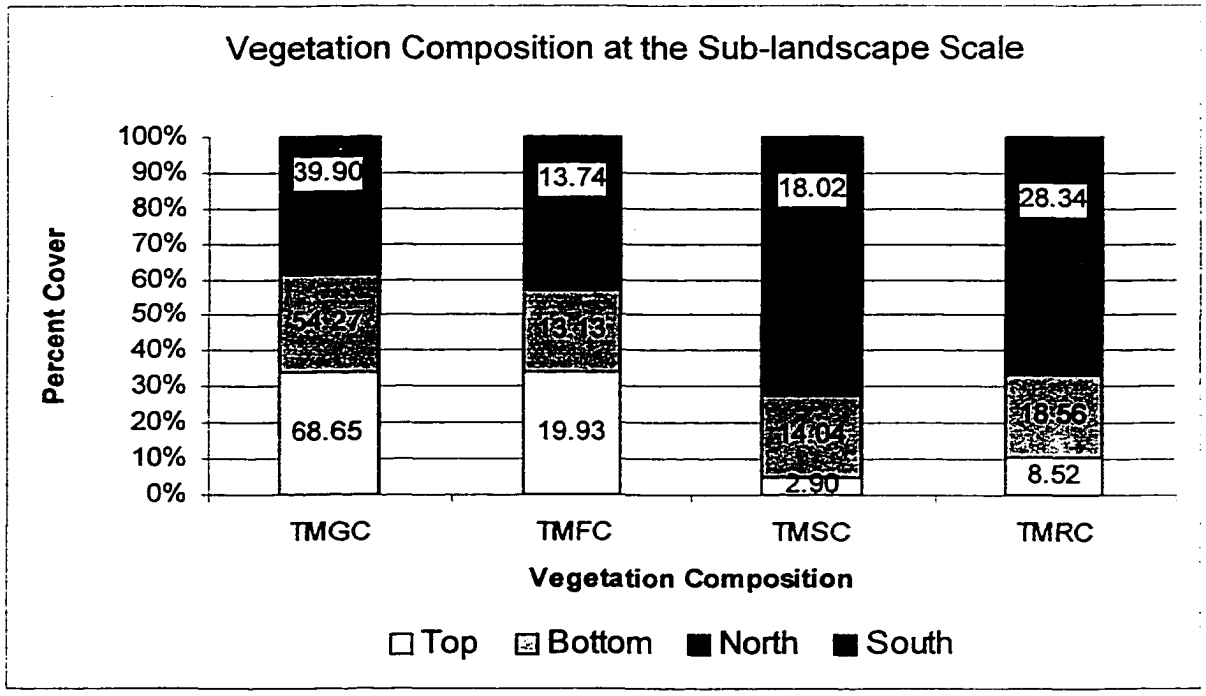
Curvilinear relationships at the landscape scale. Species diversity was also greater at intermediate levels of grass cover (r^2=0.84, p=0.005) and medium sized rocks, S5 (r^2=0.89, p=0.001). High levels of species diversity occur around 60% grass cover and 10% medium sized rocks. The graph also implies that 3% medium sized rocks corresponds to areas with little topography (low species diversity) and an area with 17% medium sized rocks corresponds to areas with the largest sized rocks, steepest slopes and greatest rock cover (low species diversity).


Species Diversity vs Total Mean Grass Cover
Species Diversity
4.0
3.5
3.0
2.5
2.0
1.5
1.0
.5
0.0
0
10
20
30
40
50
60
70
80
90
Total Mean Grass Cover (%)
Observed
Quadratic


Species Diversity vs Medium Sized Rocks
Species Diversity
4.0
3.5
3.0
2.5
2.0
1.5
1.0
.5
0.0
0
2
4
6
8
10
12
14
16
18
20
Medium Sized Rocks (%)
Observed
Quadratic

Legend Figure 7

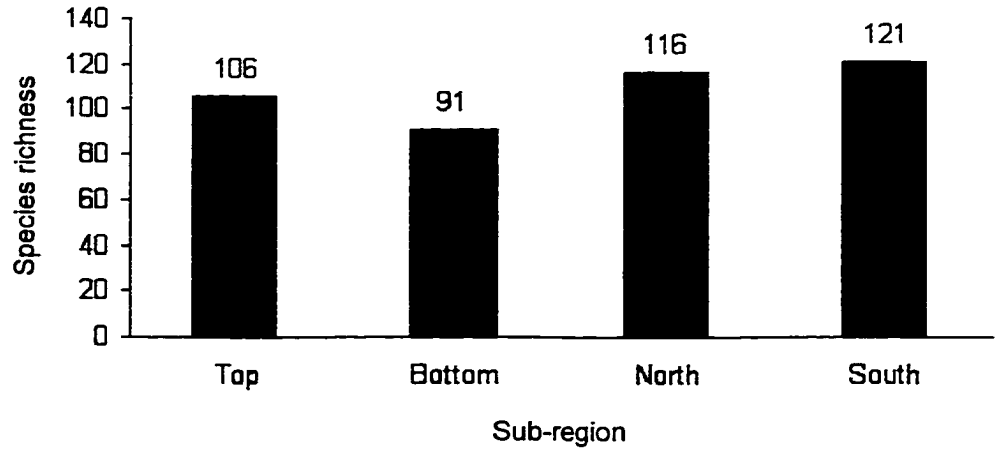
Comparison between vegetation composition variables at the sub-landscape scale at Black Mesa.


Vegetation Composition at the Sub-landscape Scale
Percent Cover
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
39.90
54.27
68.65
13.74
13.13
19.93
18.02
14.04
2.90
28.34
18.56
8.52
TMGC
TMFC
TMSC
TMRC
Vegetation Composition
Top
Bottom
North
South

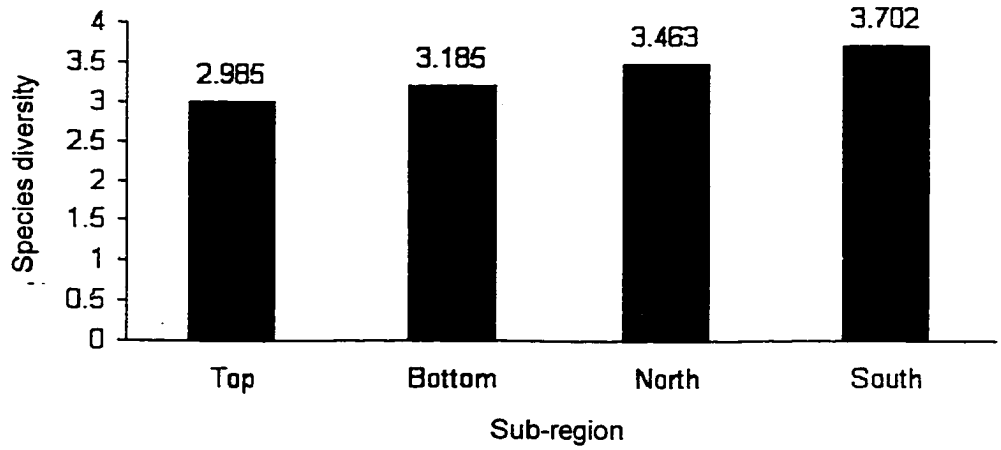
Legend Figure 8

Comparison between species richness and diversity at the sub-landscape scale at Black Mesa.

Species Richness at the Sub-landscape scale



Species Diversity at the Sub-landscape scale



Appendix I

The nine vegetation associations (clusters), including species frequencies and mean cover values.

Twinspan Clusters ---------->	A1			A2		A3		A4		A5		A6		A7		A8		A9	
Number of quadrats per cluster --->	N=18			N=12		N=14		N=11		N=4		N=8		N=3		N=18		N=13	
F=frequency / MC = mean cover -->	F	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC
SPECIES																			
Agropyron smithii var. smithii	12	-	-	1	0.1	-	-	-	-	-	-	7	5.8	-	-	4	2.6	-	-
Ambrosia psilostachya	31	-	-	2	1.3	1	0.7	5	1.2	4	6.5	2	0.3	1	1.7	10	1	7	0.5
Amorpha canescens	2	-	-	-	-	-	-	-	-	-	-	1	0.1	1	1.7	-	-	-	-
Andropogon barbinodis	15	1	0.1	1	0.1	1	0.1	4	0.4	2	1.5	-	-	-	-	2	0.6	4	0.6
Andropogon gerardii	50	-	-	7	1.7	7	5.4	4	0.4	2	2.5	6	3	3	15	15	5.6	7	2.6
Andropogon saccaroides	51	-	-	8	2.5	5	0.6	9	2.1	4	3	-	-	-	-	16	4.9	9	6.7
Arisitida oligantha	52	13	4.8	10	2.3	8	0.6	4	0.7	2	1.5	1	0.1	1	0.3	8	0.7	5	0.4
Aristida purpurea	54	12	6.8	9	4.8	9	1.5	9	1.6	1	0.3	-	-	-	-	4	0.4	10	1.7
Artemesia campestris	15	1	0.1	1	0.1	2	0.1	1	0.1	3	0.8	1	0.1	1	0.3	5	0.3	1	0.1
Artemesia filifolia	5	-	-	-	-	-	-	1	0.1	1	0.3	2	0.3	1	0.3	-	-	-	-
Artemesia ludoviciana	54	-	-	7	2.3	4	0.3	3	0.3	4	1	8	3.4	3	1	18	3.5	8	0.6
Asclepias arenaria	15	5	0.3	4	0.3	3	0.2	2	0.2	-	-	-	-	-	-	-	-	1	0.1
Asclepias asperula	10	-	-	2	0.2	4	0.3	1	0.1	-	-	2	0.3	-	-	-	-	1	0.1
Asclepias pumila	2	-	-	1	0.1	1	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Asclepias verticillata	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.1
Astragalus crassicarpus	6	2	0.1	2	0.2	2	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Aster ericoides	14	6	0.3	5	0.4	2	0.1	-	-	-	-	-	-	-	-	-	-	1	0.1
Astragalus mollissimus	43	8	0.4	7	0.6	11	0.8	8	0.7	-	-	-	-	-	-	3	0.2	5	0.4
Aster oblongifolius	1	-	-	-	-	-	-	-	-	-	-	-	-	1	0.3	-	-	-	-
Baccharis wrightii	9	-	-	2	0.2	2	0.8	-	-	3	1.8	-	-	-	-	1	0.1	2	0.2
Berlandiera lyrata	17	4	0.2	3	0.3	4	0.3	4	0.4	1	0.3	-	-	-	-	1	0.1	1	0.1
Bouteloua curtipendula	84	10	7.3	12	26	14	16	9	3.7	3	6.3	4	3.8	3	10	17	9.5	12	10
Bouteloua eriopoda	21	1	0.1	3	0.9	1	0.4	4	1.6	1	5	-	-	-	-	6	3.1	5	2.1
Bouteloua gracilis	83	18	49	12	20	11	7.6	11	17	4	14	2	0.8	-	-	12	2.7	13	8.4
Bouteloua hirsuta	43	4	0.9	5	5.9	13	19	7	18	1	0.3	1	3.8	-	-	-	-	11	4.5

Twinspan Clusters ---------->	A1			A2		A3		A4		A5		A6		A7		A8		A9	
Number of quadrats per cluster --->	N=18			N=12		N=14		N=11		N=4		N=8		N=3		N=18		N=13	
F=frequency / MC = mean cover -->	F	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC
SPECIES																			
Brickellia brachyphylla	4	-	-	-	-	-	-	-	-	-	-	2	0.3	2	0.7	-	-	-	-
Brickellia californica	27	-	-	1	0.1	1	0.1	2	0.2	-	-	3	0.4	-	-	14	1	6	0.8
Bromus tectorum	3	-	-	-	-	1	0.1	-	-	1	0.3	1	0.1	-	-	1	0.6	-	-
Buchloe dactyloides	15	-	-	-	-	1	0.1	9	17	2	0.5	1	0.6	-	-	-	-	3	0.2
Carex gravida	2	-	-	-	-	-	-	-	-	-	-	1	0.1	-	-	1	0.1	-	-
Gaura coccinea	51	17	0.9	12	1	9	0.6	6	0.6	2	0.5	-	-	1	0.3	3	0.2	1	0.1
Celtis recticulata	38	-	-	4	0.3	2	0.1	6	3.1	1	0.3	-	-	1	1.7	16	6.2	7	1.5
Ceratoides lanata	6	3	0.2	-	-	1	0.1	1	0.1	-	-	1	0.1	-	-	-	-	-	-
Cercocarpus montanus	1	-	-	-	-	-	-	-	-	-	-	-	-	1	0.3	-	-	-	-
Chamaesaracha conioides	8	7	0.4	1	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chenopodium berlandieri	2	-	-	-	-	-	-	-	-	1	0.3	-	-	-	-	-	-	1	0.1
Cheilanthes lanosa	11	-	-	1	0.1	-	-	-	-	-	-	2	0.3	-	-	7	0.4	1	0.1
Chloris verticillata	3	-	-	1	0.1	-	-	1	0.1	-	-	-	-	-	-	1	0.1	-	-
Cirsium undulatum	35	4	0.2	7	0.6	6	0.4	5	0.5	-	-	4	0.5	-	-	3	0.2	6	0.5
Conyza canadensis	6	2	0.1	1	0.1	1	0.1	1	0.1	1	0.3	-	-	-	-	-	-	-	-
Corypantha viviparia	37	16	0.9	5	0.4	6	0.4	2	0.2	-	-	1	0.1	-	-	3	0.2	3	0.2
Croton gladulosus	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0.2	-	-
Crypantha jamesii	12	4	0.2	3	0.3	5	0.4	-	-	-	-	-	-	-	-	-	-	-	-
Crypantha minima	2	1	0.1	-	-	-	-	1	0.1	-	-	-	-	-	-	-	-	-	-
Dalea aurea	12	3	0.2	-	-	6	0.4	1	0.1	-	-	-	-	-	-	1	0.1	1	0.1
Dalea candidum var. oligophyllum	7	-	-	-	-	4	0.3	2	0.2	-	-	-	-	-	-	-	-	1	0.1
Dalea enneandra	14	1	0.1	4	0.3	5	0.4	2	0.2	-	-	-	-	-	-	1	0.1	1	0.1
Dalea lanata	4	-	-	1	0.1	1	0.1	-	-	-	-	-	-	1	0.3	-	-	-	-
Dalea tenufolia	6	1	0.1	1	0.1	4	0.3	-	-	-	-	-	-	-	-	-	-	-	-
Descurainia pinnata	15	6	0.3	5	0.4	-	-	-	-	-	-	-	-	-	-	3	0.2	1	0.1

Twinspan Clusters ---------->	A1			A2		A3		A4		A5		A6		A7		A8		A9	
Number of quadrats per cluster --->	N=18			N=12		N=14		N=11		N=4		N=8		N=3		N=18		N=13	
F=frequency / MC = mean cover -->	F	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC
SPECIES																			
Digitaria cognata	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.1	-	-
Echinocereus viridiflorus	24	8	0.4	3	0.3	5	0.4	4	0.4	-	-	-	-	-	-	3	0.2	1	0.1
Elymus canadensis	16	-	-	-	-	1	0.1	-	-	2	1.5	3	0.4	2	0.7	8	0.7	1	0.1
Eragrostis intermedia	1	-	-	-	-	-	-	1	0.1	-	-	-	-	-	-	-	-	-	-
Eragrostis spectabilis	8	-	-	-	-	-	-	1	0.1	2	0.5	-	-	-	-	4	0.2	1	0.1
Eriogonum jamesii	13	-	-	1	0.1	5	0.4	2	0.2	-	-	1	0.1	-	-	1	0.1	3	0.2
Erigeron modestus	10	-	-	4	0.3	2	0.1	1	0.1	-	-	-	-	-	-	-	-	3	0.2
Erioneuron pilosum	25	10	1.7	6	0.8	3	0.2	1	0.5	1	0.3	-	-	-	-	1	0.1	3	0.2
Eriogonum tenellum	15	-	-	2	0.2	3	0.2	3	0.3	-	-	-	-	-	-	2	0.1	5	0.4
Erysimum capitatum	18	12	0.7	3	0.3	2	0.1	1	0.1	1	0.3	-	-	-	-	-	-	-	-
Euphorbia fendleri	23	-	-	3	0.3	7	0.5	5	0.5	-	-	-	-	-	-	2	0.1	5	0.4
Evax prolifera	1	-	-	-	-	-	-	1	0.1	-	-	-	-	-	-	-	-	-	-
Evolvulus nuttallianus	6	-	-	2	0.2	-	-	2	0.2	-	-	-	-	-	-	1	0.1	1	0.1
Gaillardia pinnatifida	22	6	0.3	6	0.5	3	0.2	3	0.3	-	-	-	-	-	-	-	-	3	0.2
Galium texense	4	-	-	-	-	-	-	-	-	-	-	1	0.1	-	-	3	0.2	-	-
Glossopetalon planitierum	4	-	-	1	0.4	-	-	-	-	-	-	2	3.9	-	-	1	0.3	-	-
Glycyrrhiza lepidota	1	-	-	1	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Grindelia squarrosa	37	11	0.6	8	0.7	4	0.3	6	0.6	4	1	-	-	1	0.3	2	0.1	2	0.2
Gutierrezia sarothrae	63	18	1	10	0.8	9	0.6	9	0.8	3	0.8	3	0.4	-	-	3	0.2	8	0.6
Haplopappus spinulosus	50	13	0.7	8	0.7	9	0.6	10	0.9	1	0.3	1	0.1	1	0.3	1	0.1	5	0.4
Helianthus annuus	26	8	0.7	5	0.4	6	0.4	2	0.2	2	0.5	-	-	-	-	2	0.1	1	0.1
Helioptropium convolvulaceum	5	1	0.1	2	0.2	-	-	1	0.1	-	-	-	-	-	-	-	-	1	0.1
Hilaria jamesii	27	13	11	5	3.5	-	-	5	1.6	1	1.3	-	-	-	-	1	0.6	1	0.4
Hoffmanseggia drepanocarpa	2	1	0.1	-	-	1	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Hoffmanseggia glauca	4	-	-	2	0.2	2	0.1	-	-	-	-	-	-	-	-	-	-	-	-

Twinspan Clusters ---------->	A1			A2		A3		A4		A5		A6		A7		A8		A9	
Number of quadrats per cluster --->	N=18			N=12		N=14		N=11		N=4		N=8		N=3		N=18		N=13	
F=frequency / MC = mean cover -->	F	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC
SPECIES																			
Hordeum pusillum	1	-	-	-	-	-	-	-	-	1	2.5	-	-	-	-	-	-	-	-
Hymenoxus acaulis	35	7	0.4	7	0.6	10	0.7	3	0.3	-	-	-	-	1	0.3	2	0.1	4	0.3
Hymenopappus flavescens	21	10	0.6	4	0.3	2	0.1	4	0.4	-	-	-	-	-	-	-	-	1	0.1
Hymenoxus scaposa	13	1	0.1	2	0.2	4	0.3	-	-	-	-	1	0.1	-	-	3	0.2	2	0.2
Ipomopsis laxiflora	1	-	-	1	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ipomoea leptophylla	2	-	-	-	-	-	-	-	-	-	-	-	-	1	0.3	-	-	1	0.1
Juniperus monosperma	40	2	0.1	1	0.1	8	5.1	7	3.1	1	0.3	5	6.6	1	3.3	4	0.2	10	17
Krameria lanceolata	2	-	-	-	-	1	0.1	1	0.1	-	-	-	-	-	-	-	-	-	-
Lappula redowski	14	-	-	4	0.3	1	0.1	-	-	2	0.5	-	-	-	-	7	0.6	1	0.1
Lepidium densiflorum	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.1	1	0.1
Lesquerella ovalifolia	4	-	-	-	-	3	0.2	-	-	-	-	-	-	-	-	-	-	1	0.1
Leucelene ericoides	31	11	0.8	8	0.7	7	0.5	-	-	-	-	-	-	1	0.3	1	0.1	3	0.2
Liatris punctata	37	6	0.3	6	0.5	12	0.9	7	0.6	-	-	-	-	1	0.3	2	0.1	2	0.2
Linum prenna	8	4	0.2	-	-	-	-	-	-	-	-	3	0.4	-	-	1	0.1	-	-
Linum rigidum	3	2	0.1	-	-	1	0.1	-	-	1	0.3	-	-	-	-	-	-	-	-
Lithospermum incisum	5	3	0.2	1	0.1	1	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Lycurus phleoides	10	-	-	-	-	4	0.3	-	-	2	0.5	1	0.6	-	-	1	0.3	3	2.4
Melampodium leucanthum	29	10	0.6	6	0.5	8	0.6	-	-	-	-	-	-	-	-	-	-	4	0.3
Mimosa borealis	9	-	-	-	-	3	0.5	2	0.2	-	-	-	-	-	-	1	0.1	3	0.2
Mirabilis linearis	27	6	0.3	7	0.6	5	0.4	2	0.2	2	0.5	-	-	-	-	4	0.2	2	0.2
Monarda pectinata	3	-	-	-	-	1	0.1	1	0.1	-	-	-	-	-	-	1	0.1	-	-
Muhlenbergia torreyi	28	13	1.2	5	0.4	2	0.1	5	1.2	-	-	-	-	-	-	1	0.1	1	0.1
Neptunia lutea	11	-	-	2	0.2	1	0.1	7	0.6	-	-	-	-	-	-	-	-	1	0.1
Oenothera albicaulis	7	1	0.1	2	0.2	3	0.2	-	-	-	-	-	-	1	0.3	-	-	-	-
Oenothera lavandulaefolia	2	-	-	-	-	2	0.1	-	-	-	-	-	-	-	-	-	-	-	-

Twinspan Clusters ---------->	A1			A2		A3		A4		A5		A6		A7		A8		A9	
Number of quadrats per cluster --->	N=18			N=12		N=14		N=11		N=4		N=8		N=3		N=18		N=13	
F=frequency / MC = mean cover -->	F	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC
SPECIES																			
Oenothera serrulata	1	1	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Onosmodium molle	2	-	-	-	-	-	-	-	-	-	-	1	0.1	1	0.3	-	-	-	-
Opuntia imbricaria	88	17	0.9	9	0.8	9	0.6	11	1.4	3	0.8	7	0.9	3	1	16	1.1	13	1.3
Opuntia phaeacantha	95	16	0.9	11	0.9	13	0.9	10	1.3	4	1	8	1.5	3	1	17	0.9	13	1.3
Panicum hallii	51	5	0.5	5	1.1	4	0.3	9	1.2	4	2	2	0.8	1	0.3	13	0.9	8	0.9
Panicum obtusum	22	-	-	1	0.1	1	0.4	2	0.9	3	7.5	-	-	-	-	11	4.7	5	1
Panicum virgatum	7	-	-	-	-	-	-	2	0.2	2	0.5	-	-	-	-	2	0.1	1	0.1
Penstemon albidus	9	2	0.1	1	0.1	4	0.3	-	-	-	-	1	0.1	-	-	-	-	1	0.1
Pinus edulis	1	-	-	-	-	1	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Plantago patagonica	18	3	0.2	3	0.3	1	0.1	6	0.6	1	0.3	1	0.1	-	-	2	0.1	2	0.2
Poa fendleriana	22	-	-	-	-	2	0.1	3	0.3	2	0.5	7	18	2	2	3	0.4	3	0.5
Prosopsis sp.	4	-	-	1	0.4	-	-	2	0.2	-	-	-	-	-	-	-	-	1	0.1
Prunus virginiana	3	-	-	-	-	-	-	-	-	-	-	1	0.1	-	-	1	0.1	1	0.1
Psoralea tenuifolium	46	9	0.5	4	0.3	7	0.5	9	0.8	1	0.3	2	0.3	1	0.3	7	0.6	6	0.5
Ptelea trifoliata	21	-	-	1	0.1	3	0.5	2	0.6	2	1.5	7	7.5	1	0.3	3	2.3	3	0.5
Quincula lobata	2	-	-	-	-	-	-	2	0.2	-	-	-	-	-	-	-	-	-	-
Ratibida columnifera	43	15	0.8	7	0.6	5	0.4	5	0.5	1	0.3	2	0.3	-	-	7	0.4	1	0.1
Ratibida tagetes	5	-	-	1	0.1	-	-	1	0.1	-	-	1	0.6	-	-	1	0.1	1	0.1
Rhus aromatica var. pilosissima	62	-	-	3	0.6	8	0.9	7	1.5	3	4	8	19	3	43	17	11	13	8.8
Ribes cereum	1	-	-	-	-	-	-	-	-	-	-	1	0.6	-	-	-	-	-	-
Rubus deliciosus	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sapindus saponaria var. dummondii	12	-	-	1	0.1	-	-	-	-	-	-	-	-	-	-	8	4.6	3	0.2
Schedonnardus paniculatus	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Schizachyrium scoparium	30	-	-	3	0.6	9	7	2	0.2	1	1.3	3	1.4	3	5	5	0.5	4	0.3
Senecio douglasii var.	19	5	0.3	2	0.2	2	0.1	7	0.6	-	-	-	-	-	-	1	0.1	2	0.2

Twinspan Clusters ---------->	A1			A2		A3		A4		A5		A6		A7		A8		A9	
Number of quadrats per cluster --->	N=18			N=12		N=14		N=11		N=4		N=8		N=3		N=18		N=13	
F=frequency / MC = mean cover -->	F	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC
SPECIES																			
Senecio plattensis	1	-	-	-	-	-	-	-	-	-	-	1	0.1	-	-	-	-	-	-
Setaria leuchopila	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	0.9	-	-
Sitanion hystrix	47	14	0.8	10	0.8	6	0.4	2	0.2	1	0.3	1	0.1	1	0.3	9	0.5	3	0.9
Solidago missouriensis	2	-	-	-	-	-	-	-	-	1	0.3	-	-	-	-	1	0.1	-	-
Solidago mollis	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0.3	2	0.2
Sophora nuttalliana	33	10	1	6	0.5	4	0.3	5	0.5	-	-	2	0.3	-	-	3	0.6	3	0.2
Sorghastrum nutans	4	-	-	-	-	-	-	-	-	-	-	1	0.1	-	-	2	0.3	1	0.1
Sphaeralcea angustifolia	5	2	0.1	-	-	-	-	-	-	1	0.3	-	-	-	-	1	0.1	1	0.1
Sphaeralcea coccinea	59	18	1	12	1	7	0.5	6	0.6	1	0.3	1	0.1	-	-	9	0.5	4	0.3
Sporobolus cryptandrus	58	15	3.7	7	1.7	3	0.9	7	0.6	4	9	-	-	-	-	16	1.8	6	0.5
Stephanomeria juncea	4	-	-	-	-	-	-	1	0.1	-	-	-	-	1	0.3	-	-	2	0.2
Stephanomeria pauciflora	14	3	0.2	2	0.2	-	-	2	0.2	-	-	1	0.1	-	-	5	0.3	1	0.1
Stipa comata	3	-	-	-	-	1	0.1	-	-	-	-	-	-	-	-	1	0.1	1	2.3
Thelesperma megapotamicum	39	7	0.4	10	0.8	12	0.9	3	0.3	1	0.3	1	0.1	-	-	-	-	6	0.5
Toxicodendron radicans	3	-	-	-	-	-	-	-	-	-	-	2	1.4	-	-	-	-	1	0.1
Tragopogon dubius	11	3	0.2	2	0.2	5	0.4	-	-	1	0.3	-	-	-	-	-	-	1	0.1
Tradescantia occidentalis	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.1
Tragia ramosa	36	1	0.1	3	0.3	5	0.4	3	0.3	2	0.5	2	0.3	1	0.3	12	0.7	8	0.6
Tridens muticas	22	-	-	3	0.3	1	0.7	1	0.1	3	3	-	-	1	0.3	11	3.8	3	0.2
Unknown 100	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.1	-	-
Unknown 203 (Asclepiadaceae)	1	-	-	1	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unknown 210 (Fabaceae)	10	2	0.1	1	0.1	-	-	-	-	-	-	-	-	-	-	7	0.4	-	-
Unknown 411 (Poaceae)	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	0.7	-	-
Unknown 421 (Euphorbiaceae)	2	-	-	-	-	-	-	1	0.1	-	-	-	-	-	-	-	-	1	0.1
Unknown 422 (Euphorbiaceae)	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.1

Twinspan Clusters ---------->	A1			A2		A3		A4		A5		A6		A7		A8		A9	
Number of quadrats per cluster --->	N=18			N=12		N=14		N=11		N=4		N=8		N=3		N=18		N=13	
F=frequency / MC = mean cover -->	F	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC	F	MC
SPECIES																			
Unknown 424	1	-	-	1	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unknown 444 (Poaceae)	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0.2	1	0.1
Unknown 520 (Asteraceae)	2	2	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unknown 600 (Asteraceae)	1	-	-	-	-	-	-	1	0.1	-	-	-	-	-	-	-	-	-	-
Unknown 10 (Fabaceae)	3	1	0.1	-	-	1	0.1	-	-	-	-	1	0.1	-	-	-	-	-	-
Verbena bipinnatifida	27	14	0.8	8	0.7	1	0.1	1	0.1	1	0.3	1	0.1	-	-	-	-	1	0.1
Vicia americana	15	2	0.1	3	0.6	-	-	2	0.2	-	-	2	0.3	-	-	5	0.3	1	0.1
Vitus vulpina	1	-	-	-	-	-	-	-	-	-	-	1	0.1	-	-	-	-	-	-
Vulpia /Festuca octoflora	7	-	-	2	0.2	1	0.1	3	0.6	-	-	-	-	-	-	-	-	1	0.1
Yucca glauca	67	11	1.1	11	1.6	12	2.7	8	0.7	2	0.5	4	0.5	2	0.7	6	0.3	10	1.1
Zinnia grandiflora	34	8	0.4	3	0.3	5	0.4	7	0.6	2	0.5	1	0.1	-	-	3	0.2	5	0.4

Appendix II

Detailed description of the nine vegetation associations.

Association 1 (A1): Bouteloua gracilis - Hilaria jamesii

This vegetation association dominated the top of Black Mesa, excluding most areas close to or at the rim. A1 was dominated by Bouteloua gracilis and Hilaria jamesii was a co-dominant species. Associate species included Bouteloua curtipendula, Arisitida oligantha and Aristida purpurea. Several forb species and two grass species occurred on the top more frequently than in any other association including Chamaesaracha conioides, Corypantha viviparia, Echinocereus viridiflorus Erysimum capitatum, Gutierrezia sarothrae, Helianthus annuus, Hymenopappus flavescens, Leucelene ericoides, Ratibida columnifera, Sophora nuttalliana Verbena bipinnatifida, Erioneuron pilosum and Muhlenbergia torreyi. This association had the highest mean grass cover and the lowest values for evenness, mean shrub cover and mean rock cover.

Association 2 (A2): Bouteloua curtipendula - Bouteloua gracilis

This vegetation association dominated areas close to or at the rim of Black Mesa. Areas that exist on the southern slopes occurred above the lower member of the Dakota Formation (see map) and are virtually free from exposed rocky slopes and outcrops. A2 was equally dominated by Bouteloua curtipendula and Bouteloua gracilis. Associate species included Bouteloua hirsuta and Aristida purpurea. Two forb species, Glycyrrhiza lepidota and Ipomopsis laxiflora were only found in this association while Mirabilis linearis occurred more frequently near the rim than any other association. This association had the highest mean forb cover.

Association 3 (A3): Bouteloua hirsuta - Bouteloua curtipendula /Juniperus monosperma

This vegetation association was located on the mid to lower slopes of Black Mesa, where Juniperus monosperma is scattered. A3 was equally dominated by Bouteloua hirsuta and Bouteloua curtipendula. Juniperus monosperma was a co-dominant species. Associate species included Schizachyrium scoparium and Andropogon gerardii. Geologically, A3 was located on the southern slopes below the lower member of the Dakota Formation and on the northern slopes below the Cheyenne Sandstone of the Purgatoire Formation. The forb species, Oenothera lavandulaefolia, was only found in this association while several other forb species occurred on the mid to lower slopes more frequently than in any other association including Hymenoxus acaulis, Hymenoxus scaposa, Liatris punctata, Oenothera albicaulis and Penstemon albidus.

Association 4 (A4): Bouteloua hirsuta - Bouteloua gracilis - Buchloë dactyloides

This vegetation association dominated the base of Black Mesa and transition areas grading into lower foot slopes of A3. A4 was equally dominated by Bouteloua hirsuta, Bouteloua gracilis and Buchloë dactyloides. Associate species included Bouteloua curtipendula, Celtis reticulata and Juniperus monosperma. These associated species were mostly found in transition areas. The grass species Eragrostis intermedia and forb species Quincula lobata were only found in this association while the base contained many forb species that occurred more frequently than any other association including Plantago patagonica, Psoralea tenuifolium, Senecio douglasii, Festuca octoflora and Zinnia grandiflora.

Association 5 (A5): Bouteloua gracilis - Sporobolus cryptandrus / Panicum obtusum

This vegetation association dominated the middle northern slopes above the lower member of the Dakota Formation (similar topographic location as A2 on the southern slopes). A5 was dominated by Bouteloua gracilis, and Sporobolus cryptandrus and Panicum obtusum were co-dominant species. Associate species included Ambrosia psilostachya and Bouteloua curtipendula. The grass species Hordeum pusillum was only found in this association while forb species Haplopappus spinulosus occurred more frequently in A5 than any other association. This association had the highest species evenness value.

Association 6 (A6): Rhus aromatica - Ptelea trifoliata / Poa fendleriana

This vegetation association dominated the canyons and more sheltered areas on the north side of Black Mesa. Rhus aromatica and Ptelea trifoliate dominated the woody vegetation and Poa fendleriana, a C3 grass, dominated the understory. Associate species included Juniperus monosperma, Agropyron smithii, Glossopetalon planitierum, Bouteloua curtipendula and Bouteloua hirsuta. Shrub species Amorpha canescens and Ribes cereum and forb species Senecio plattensis and Vitus vulpina were only found in this association.

Association 7 (A7): Rhus aromatica - Andropogon geradii

This vegetation association was located on the steep north facing slopes (and talus) of Black Mesa near the rim. A7 was dominated by Rhus aromatica and Adropogon geradii was a co-dominant species. Associate species included Bouteloua curtipendula and Schizachyrium scoparium. The shrub species Cercocarpus montanus was only found in this association. A7 had the highest mean shrub cover and the lowest values for species richness, species diversity and mean forb cover.

Association 8 (A8): Rhus aromatica / Bouteloua curtipendula

This vegetation association dominated the steep south facing slopes near the rim above the lower member of the Dakota Formation. With a limited number of occurrences found on the northern slopes, this association was located above and below the lower member of the Dakota Formation. A8 was dominated by Rhus aromatica. Bouteloua curtipendula was the co-dominant species. Associate species included Celtis recticulata, Andropogon geradii and Andropogon saccaroides. A8 has a complex topography and contains many rocks (talus) and taller grasses. It is equivalent to A7 in terms of topography and dominant species even though A7 and most of A8 occur on opposite sides of Black Mesa. A8 occurs on steep south facing slopes and A7 occurs on steep north facing slopes with a significant increase in the percent cover of Rhus aromatica. Forb species Croton gladulosus and grass species Digitaria cognata and Setaria leuchopila were only found in this association. The steep south facing slopes contained many species of grasses, forbs and shrubs that occurred more frequently than any other association including Bouteloua eriopoda, Tridens muticas, Artemesia ludoviciana, Galium texense, Lappula redowski, Brickellia californica and Sapindus saponaria. A8 had the highest species diversity value.

Association 9 (A9): Juniperus monosperma / Bouteloua curtipendula

This vegetation association dominated the drainage draws on the southern slopes and the mid to lower northern slopes. These areas contained a complex topography with many rocks and taller grass species. A9 was dominated by Juniperus monosperma and Bouteloua curtipendula was a co-dominant species. Associate species included Rhus aromatica, Bouteloua gracilis and Andropogon saccaroides. Forb species Tradescantia occidentalis was only present in this association while grass species Andropogon barbinodis occurred more frequently in A9 than in any other association. This association had the highest species richness value and highest mean rock cover.

Chapter III

Environmental Factors Influencing Structure and Composition of Vegetation in a Semi-arid Environment: Black Mesa, Cimarron County, Oklahoma

Abstract

Situated in the far northwest corner of Cimarron County, Oklahoma, this research focuses on a semi-arid mesa environment lying at a crossroads defined by parts of four major biomes, each contributing to the local species richness and diversity. Using a combination of detrended correspondence analysis and canonical correspondence analysis, the overall goal of this research is to analyze ecological patterns as related to environmental gradients. Additionally, this research will explore the main environmental factors contributing to patterns of species richness and diversity at the site level, adding to the general body of literature in arid and semi-arid environments.

The use of multivariate analysis in montane and arid environments has shown that landforms dictate the scale at which environmental factors affect the structure and composition of vegetation. The effects of temperature, precipitation and insolation on vegetation along altitudinal gradients tend to be more significant in montane landscapes. In contrast, the effects of surface rock cover, soil texture and nutrient availability on vegetation along slope gradients tend to be more significant in arid and semi-arid landscapes. Studies using multivariate analysis in arid landscapes have yet to focus on environmental factors affecting vegetation structure and composition, as well as species richness and diversity, in mesa environments.

Analyses showed that temperature and precipitation at Black Mesa was not considered a major factor affecting the distribution of vegetation at the scale that the data were analyzed. Instead, vegetation structure and composition at smaller scales were most affected by topography and geomorphology (slope,

rock size, rock cover and sand content) and nutrient availability (nitrogen, phosphorus, potassium). The greatest species richness and diversity was found in areas with moderate habitat structure containing a mixture of shrubland and grassland species. These environments contained medium sized rocks, moderate slopes and moderate amounts of surface rock cover and nutrients.

Increased habitat structure resulted in higher species diversity and decreasing habitat structure resulted in higher species richness. In addition, the abundance of woody and tall grass species was mostly influenced by the presence of large rocks, increased slopes and soil texture and higher nutrient availability. The abundance of shorter and mixed grass species was mostly influenced by increased rock cover, soil depth and pH, finer textured soils and decreased rock size.

Keywords: Detrended correspondence analysis, canonical correspondence analysis, environmental gradients, vegetation-environment relationships, species richness, species diversity, topo-edaphic effects, nutrient availability, scale

Nomenclature: Flora of the Great Plains (Great Plains Flora Association 1986).

Introduction

Environmental gradients are commonly used for analyzing spatial patterns of vegetation and the relationship between vegetation and the environment (Kent & Coker 1992; Jongman et al. 1995). The ability to summarize and classify ecological patterns has increased with the development of multivariate techniques (Gauch 1982; Keddy 1991; McGarigal et al. 2000). These techniques are related to direct and indirect gradient analysis, two primary methods for the study of species response along environmental gradients.

Indirect gradient analysis, typically referred to as unconstrained ordination, is performed independently of environmental factors and uses mathematical methods to exploit the major underlying structure of the data in a few abstract dimensions by examining the variation within it (Austin 1985). One of the most widely used unconstrained ordination techniques is detrended correspondence analysis (DCA; Hill & Gauch 1980). It is an improved eigenvector ordination technique based on correcting two main faults of reciprocal averaging or correspondence analysis, the arch effect and gradient compression (Gauch 1982). Because only community data are analyzed, the interpretation of the strength of the environmental factors is performed visually by the researcher and statistically through the use of multivariate statistics (ter Braak 1988).

In contrast, direct gradient analysis was developed as a research tool by Whittaker (1967) and explores the distribution of species along known environmental gradients. More recently, canonical (constrained) ordination methods, referred to as multivariate direct gradient analysis (ter Braak 1986; ter Braak & Prentice 1988), detect patterns of variation in species and environmental

data. These represent a more efficient way of analyzing variation in community composition and structure than attempting to organize single species distributions with environmental factors as in true direct gradient analysis. The main purpose of canonical ordination is to simplify the interpretation of complex data sets by organizing samples along gradients defined by combinations of interrelated variables (ter Braak 1987). These methods are designed to extract environmental gradients from large ecological data sets where the ordination axes are linear combinations of environmental variables (ter Braak & Verdonschot 1995).

Canonical correspondence analysis (CCA; ter Braak 1986) is the best canonical ordination method that elucidates the relationships between species composition and the environment (ter Braak & Prentice 1988; McGarigal et al. 2000) and has become the most widely used gradient analysis technique (Palmer 1993; McCune 1997). Until recently, few studies have combined the use of both constrained (CCA) and unconstrained (DCA) ordination techniques (Allen et al. 1991; Velázquez 1994; Ferreyra et al. 1998). Using both techniques adds value when interpreting significant compositional and environmental gradients by filling gaps in the qualitative and quantitative analyses.

For instance, Allen et al. (1991) used DCA to determine dominant compositional gradients related to known site variables using CCA at different localities in southern Rocky Mountain forests. Velázquez (1994) used DCA to identify outliers and CCA to find variables that best explained the variance in the species and environment data on two volcanoes in Mexico. Additionally, the final results obtained by DCA and CCA were compared to see whether environmental

variables were overlooked. Ferreyra et al (1998) investigated floristic gradients with DCA and environmental gradients with CCA in northwestern Patagonia, Argentina.

In studies using multivariate analysis, the scale of the study will determine which gradients are analyzed to explain the variance in the data. Larger scale studies often focus on climatic or elevation gradients while smaller scale studies usually focus on topographic and edaphic factors. For example, Witkowski and O'Conner's (1996) regional scale study of African savannas showed that precipitation, temperature and solar radiation had a greater influence on composition and structure of vegetation than topo-edaphic factors. Cox and Larson (1992) discovered that latitude and climate gradients affected regional patterns of vegetation on talus slopes of the Niagara Escarpment, while complex soil gradients explained local scale patterns. Duckworth et al. (2000) investigated the main vegetation gradients in calcareous grasslands of Atlantic Europe and showed that climate controlled the large-scale distribution of vegetation while topo-edaphic factors were important at finer scales.

Multivariate direct gradient analysis has typically been employed in montane (Tang & Ohsawa 1997; Hsieh et al. 1998; Ferreyra et al. 1998; Kirkpatrick & Bridle 1998; Vazquez & Givnish 1998) and arid environments (Cornelius et al. 1991; Parker 1991; McAuliffe 1994; Valverde et al. 1996). Given that montane environments contain larger scale landforms than arid environments, underlying gradients that account for most of the variation in species data are related to larger scale gradients. The effects of temperature, precipitation and insolation on vegetation along altitudinal gradients are more

significant in montane landscapes. In contrast, the effects of surface rock cover, soil texture and nutrient availability on vegetation along slope gradients are more significant in arid and semi-arid landscapes.

In montane environments, Kirkpatrick and Bridle (1998) showed that climatic factors had the greatest influence on vegetation patterning in southeast Australia. Ferreyra et al. (1998) found that available moisture (defined by longitude), temperature (defined by altitude) and insolation (defined by aspect) were the major factors affecting vegetation distribution in northwestern Patagonia, Argentina. Similarly, several studies have investigated climatic effects related to elevation in describing broad vegetation zones (Allen et al. 1991; Ghazanfar 1991; Velázquez 1994; Tang & Ohsawa 1997; Hsieh et al. 1998; Vazquez & Givnish 1998).

In arid environments, Parker (1991) discovered that topographic and soil texture gradients best explained the distribution and richness of vegetation on bajada sequences in Organ Pipe Cactus National Monument in the northern Sonoran Desert. Also in the Sonoran Desert, McAuliffe (1994) showed that the underlying geology and landform type determined changes in vegetation composition. Furthermore, the highest species diversity was encountered on steeper slopes with coarser texture. The role of geologic surface structure and soil texture was also a controlling factor in the Negev Desert (Olvig-Whittaker et al. 1983; Ward et al. 1993).

Increased soil heterogeneity, defined by the degree of stoniness and texture, was shown to be a major factor allocating moisture and increasing species richness. In the southern Chihuahuan Desert, Valverde et al. (1996)

showed that vegetation distribution was significantly correlated with land form type and increases in species richness was related to increases in landscape heterogeneity. Montaña (1990), working in the Mapimi subdivision of the Chihuahuan Desert, showed that species distribution and diversity was directly related to habitat structure defined by increased soil texture and surface rock cover. In the Jornada del Muerto Basin in south-central New Mexico, Cornelius et al. (1991) demonstrated that high species diversity was related to available nitrogen and water, defined by increased soil texture. Several other studies have shown that species composition was significantly correlated with finer scale topographic, geomorphic and edaphic factors (Ayyad 1981; Ezcurra et al. 1987; Montaña 1988; Wondzell et al. 1990; Wondzell et al. 1996).

Research using multivariate analysis in montane and arid environments has shown that landforms dictate the scale at which environmental factors affect the structure and composition of vegetation. Studies using multivariate analysis in arid landscapes have yet to focus on environmental site factors affecting vegetation structure and composition, as well as species richness and diversity, in mesa environments. Situated in the far northwest corner of Cimarron County, Oklahoma, this research focuses on a semi-arid mesa environment lying at a crossroads defined by parts of four major biomes, each contributing to the local species richness and diversity. Using a combination of DCA and CCA, the overall goal of this research is to analyze ecological patterns as related to environmental gradients. Additionally, this research will explore the main environmental factors contributing to patterns of species richness and diversity at

the site level, adding to the general body of literature in arid and semi-arid environments.

Study area

This study encompasses an area of about 18 sq km and includes Black Mesa and its surrounding landscape. Black Mesa is located in the far northwest corner of Cimarron County, Oklahoma, and is the eastern most extension of Mesa de Maya, a lava-capped plateau approximately 72 km in length and 600 m to 10 km wide (Rothrock 1925) (Figure 1). The study area contains the 648 hectares denoted as Black Mesa Nature Preserve, which is jointly administered by the Oklahoma State Park System and The Nature Conservancy. The remaining 1152 hectares (64% of the study area) is in private ownership.

The Mesa de Maya has long been recognized as a biogeographically unique region on the Great Plains. In Oklahoma, the eastern most extension of the Rocky Mountain Foothills meets portions of the western most extension of the Eastern Deciduous Forest. Mixed into these two biomes is the vegetation of the Great Plains and the Desert Southwest (Rogers 1949). The diversity of vegetation at Black Mea results from complex spatial patterning from a combination of geomorphic and topographic factors. Thirty-one state rare species (23 plants and 8 animals) are found at Black Mesa (The Nature Conservancy 1998).

Climate

The climate of Black Mesa is semiarid and continental. The average annual precipitation in Kenton (2 miles south of Black Mesa) is 43.5 cm with most occurring during the spring and summer months (Schoff 1943; Murphy et al. 1956). The average annual mean temperature at Kenton is 12.2°C. The months

of July (25.1°C average) and August (24.1°C average) are the warmest while December (1.1°C average) and January (0.9°C average) are the coldest (Schoff 1943). On average, there are only four days a year when the temperature dips below -17.8°C and cold spells are short in duration. Temperatures of over 32.2°C normally occur about 60 days a year, but the heat is seldom oppressive because of the elevation and the low humidity (Murphy et al. 1956).

Moisture stress is exacerbated by daily windy conditions with maximum velocities occurring in the afternoon and subsiding during the evening. In the winter, dry winds from the Rocky Mountains blow across Black Mesa while potential moisture from the Gulf of Mexico arrives during the spring, summer and early fall (Schoff 1943; Murphy et al. 1956).

Geology

Black Mesa averages 168 meters of relief with an average elevation of 1494 meters on top and 1326 meters at the base. Mesa de Maya, including Black Mesa, is an example of inverted topography that represents 250 million years of visible geologic history (Suneson & Luza 1999). It consists of layered deposits of sandstone, shale, clay and limestone. These sedimentary deposits are capped by a resistant layer of dark brown and black basalt, giving Black Mesa its name (Rogers 1949). The near-vertical slopes below the lava cap are littered with angular basalt talus fragments while sandstone and shale slopes are littered with large sandstone blocks. The source of this Late Tertiary basalt is from Piney Mountain, an extinct volcano, which flowed two to five million years ago (Rothrock 1925). The geologic stratigraphy of Black Mesa, from higher to

lower elevation consists of: Raton Basalt (Tb), Ogallala Formation (To), Dakota Formation (Kd), Purgatoire Formation (Kp) and the Morrison Formation (Jm) (Figure 2).

The Raton Basalt increases in thickness from approximately 15 meters (m) to about 26 m at the New Mexico/ Oklahoma border. The Ogallala Formation is a moderately permeable mixture of braided stream deposits containing sand, silt, clay, gravel and limy sediments (Schoff 1943; Stovall 1943). The bulk of the formation is composed of fine-grained, well-sorted sand that varies in thickness from 23 m to 61 m (Rothrock 1925). The Dakota Formation is composed of lower sandstone, middle shale and upper sandstone members (Schoff 1943; Stovall 1943). The lower sandstone member of the Kd is the upper of two massive sandstone beds that are prominent features of Mesa de Maya (the lower of the two massive sandstone beds is part of the Kp). It also is the caprock of adjacent mesas and buttes (Rothrock 1925). The maximum height of the Kd is 56 m (Stovall 1943).

The Purgatoire Formation consists of the Kiowa shale overlying the Cheyenne sandstone and ranges in thickness from approximately 12 m to 36 m (Rothrock 1925; Stovall 1943). The Kiowa shale is a dark gray to black fossiliferous shale which grades into a sandy shale and platy sandstone (Rothrock 1925). The Cheyenne sandstone is the lower of two massive sandstone beds visible on Mesa de Maya. It is buff to white in color, course-grained and poorly structured (Rothrock 1925). The Morrison Formation is the most widespread formation with a maximum thickness of 142 m (Stovall 1943). It is found on the lower slopes and base of Black Mesa and is composed of

variegated shale, clay, marl, sandstone, conglomerate and limestone. Some dolomite and quartzite are also present (Schoff 1943).

Soils

Soils at Black Mesa are Entisols (Gray and Roozitalab 1976), which are mostly shallow and rocky, and occur on steep slopes. Surface soils (A horizon) have little organic matter accumulation and show little or no evidence of soil formation. Parent material occurs immediately below the A-horizon because clay or organic matter has been lost by eluviation. The major soil types at Black Mesa, from higher to lower elevation, are Apache (top), Rough stony land (mid-to-upper slopes), Travesilla (mid-to-lower slopes) and Berthoud (base) (Murphy et al. 1956; Gray and Roozitalab 1976).

Apache stony clay loam (Aa) varies from a few inches to several feet in depth and is found on the top of Black Mesa. These soils are composed mostly of clay from the weathering of basalt, along with scattered fragments of basalt (Rogers 1953, 1954; Gray and Galloway 1969). The soils that occupy the upper to mid slopes of Black Mesa are Rough stony land (Rf), which is a mixture of transported sand and gravel with a significant amount of clay derived from weathered basalt.

The topography is a combination of talus, scattered rock fragments and steep sandstone escarpments. Rough stony land contains a very small amount of true soil since slopes range from about ten percent to nearly vertical cliffs. Upper slopes are scattered with basalt blocks with an increasing abundance of sandstone blocks further down slope (Murphy et al. 1956; Gray and Galloway

1969). Travesilla stony loam (Ta) and Berthoud loam soils (Bc) are found on the lower slopes and flat areas below Rf soils and develop from loose colluvium from the upper slopes. Ta soils occur on 2 to 12 percent slopes and are relatively shallow. Bc soils are the deepest, most permeable and mature soils and occur on 3 to 5 percent slopes. In many places the Ta soils slope toward the non-stony, gentle foot slopes of the Bc soils (Murphy et al. 1956; Gray and Galloway 1969).

Vegetation

Rogers (1949) described four major vegetation types at Mesa de Maya: prairie, foothill, Rocky Mountain and riparian. Prairie vegetation occurs on mature soils with minimal erosion (Rogers 1953) and is dominated by Bouteloua gracilis and Bouteloua hirsuta. Bouteloua hirsuta is more abundant in sandier areas whereas Bouteloua gracilis is more plentiful throughout the study area (Bruner 1931; Blair and Hubbell 1938). In areas of greater water availability, Andropogon barbinodis, Andropogon gerardii, Andropogon saccaroides and Schizachyrium scoparium dominate.

Rocky Mountain and foothill vegetation is limited to canyons, talus and mesa slopes where erosion, deposition, accumulation of moisture, shading, slope and other environmental factors produce a variety of microhabitats (Rogers 1954). The dominant woody plants characteristic of these areas include: Celtis reticulata, Juniperus monosperma, Ptelea trifoliata, Rhus aromatica and Sapindus saponaria. Thick stands of woody vegetation grow near talus, drainage and canyon areas and are frequently interrupted by large basalt or sandstone blocks. Vegetation cover ranges from nearly impenetrable thickets,

especially on north facing slopes, to less dense woody vegetation interspersed with prairie vegetation on south facing slopes (Rogers 1954). Although no riparian vegetation was included in this study, Rogers (1949) showed that cottonwood and willow species dominated.

Methods

Data Collection

Vegetation data were collected from three permanent transects traversing Black Mesa. Each transect was spaced approximately one mile apart and oriented approximately perpendicular to contour lines. These transects were designated as east, central and west and were composed of 26, 26 and 21 quadrats respectively. Each quadrat measured 10 x 10 meters and was placed at 75 meter intervals along the transect. In order to increase the sample size, five additional temporary transects totaling 28 quadrats were located on the slopes in spatially complex areas (Figure 3).

Quadrats along each permanent transect were sampled twice during the 1998 growing season from May through October and once in May (1999). Temporary transects were sampled once during the 1998 growing season. The first quadrat for slope transects was placed just below the rim of the Mesa and extended downward. Transects on the top began at the north rim and ended at the south rim. All species in the quadrat were recorded and percent cover (abundance) was visually estimated using the following scale: 1, 5, 10, 20, ... , 100.

In order to evaluate the effects of temperature and precipitation at Black Mesa, a total of five meteorological stations were established along the east transect from March 1998 through September 2000 (30 months) (Figure 3). One station was located on the top and center of Black Mesa and two stations (one on each side of Black Mesa) were located several hundred meters from its base. These stations collected temperature and precipitation. The horizontal distance

between the northern and southern base stations is approximately 2.5 kilometers. Two additional stations, collecting precipitation, were located on the northern and southern slopes of Black Mesa, halfway between the base and rim.

A Stowaway ®XTI data logger (Onset Computer Corporation) with external probe was used to collect temperature data. It was mounted one meter above the ground in a waterproof container and attached to a tripod and suspended below a protective shield. Temperature was averaged over five minute time intervals and 30-month mean totals calculated. A HOBO Event data logger (Onset Computer Corporation) was used to collect precipitation data. It recorded the number of tips from a leveled tipping bucket rain gauge (Novalynx Corporation) with an orifice eight inches in diameter and 30-month mean totals calculated. In the event that the loggers for either temperature or precipitation did not obtain data, data were only analyzed for portions of each month where all sites recorded data. Patterns of temperature and precipitation, rather than absolute values were important for this study. Finally, a paired samples t-test was performed on mean temperature and precipitation values for the entire 30-month period (95% confidence interval) so that topographic effects on temperature and precipitation could be compared.

Because rock fragments and boulders are an integral part of Black Mesa, percent rock cover for each plot was visually estimated within each quadrat. In addition, percent rock cover within seven rock size classes (S1: < 78 cm^2; S2: 78 - 235 cm^2; S3: 235 - 392 cm^2; S4: 392 - 785 cm^2; S5: 785 - 1570 cm^2; S6: 1570 - 2355 cm^2; S7: > 2355 cm^2) was visually estimated with the same scale. Maximum rooting depth (soil depth) was calculated using a 30 cm steel spike.

The spike was driven into the ground at three locations (NW, center, SE) in each quadrat and average depth calculated. In addition, a 15 cm x 15 cm hole was dug at these three locations at a depth of 30cm. From each hole, a profile soil sample was collected.

A fertility analysis (OSU extension fact sheet F-2901 1998) and textural analysis (North American Proficiency Testing Program 1997) were performed at the Soil, Water and Forage Analytical Laboratory (SWFAL) at Oklahoma State University, Stillwater, Oklahoma. Parameters measured were nitrogen, phosphorus, potassium and pH levels and percent sand, silt and clay. Percent slope of each quadrat was determined using a Suunto clinometer and aspect using a Suunto compass adjusted for magnetic north. Elevation of each quadrat was determined using a Thommen® Digital Altronic Traveller® Altimeter. Universal Transverse Mercator (UTM) coordinates were obtained for each quadrat using a global positioning system.

Data Analysis

Indirect gradient analysis was performed on the species cover data using detrended correspondence analysis (DCA: detrending by segments; nonlinear rescaling of axis; downweighting of rare species; Hill and Gauch 1980; McCune and Mefford 1997). After the DCA ordinations were inspected for outlier effects, they were used to identify and describe patterns among species and quadrats in order to reveal the strongest gradients in the data. Using the Statistical Package for the Social Sciences (SPSS 1998), the quadrat axis scores were correlated against the environmental data in order to better interpret the ordination axes.

Species richness (S), evenness (E; Pielou 1977) and Shannon's diversity index (H'; Shannon and Weaver 1949) were calculated at each scale using PC-ORD (McCune and Mefford 1997) and relationships among the environmental variables tested. Patterns of species richness and diversity were also observed in ordination space at the site level. Because the measurement of species diversity is often synonymous with species richness, a brief explanation follows.

Species diversity is composed of two components, the number of species in a given area (species richness) and equitability of their abundance (species evenness) (Peet 1974; Magurran 1988). The Shannon index of diversity (H') has been the most widely used index in community ecology and is defined as $H' = - \Sigma p_i \ln p_i$ where H' describes the average degree of uncertainty of predicting the species of an individual picked at random from the area or habitat. This uncertainty increases both as the number of species increases and as the individuals are distributed more equitably among the species already present. The parameter p_i is the decimal fraction of individuals belonging to the ith species (Ludwig and Reynolds 1988; Cox 1996). The most common evenness index used by ecologists is $E = H' / \ln (S)$ and is similar to J' of Pielou (1977).

Direct gradient analysis was used to find a linear combination of environmental variables that best explained the variance of sites and species. Canonical correspondence analysis (CCA; ter Braak 1998) was used to analyze a secondary matrix of 20 variables (elevation, rock cover, slope, northness, eastness, soil depth, seven rock size classes, three texture variables, four fertility variables), 159 species and 73 quadrats. Included in the analysis, a forward selection of variables was used to determine the significance of each

environmental variable. A weighted correlation matrix was used to determine environmental relationships among environmental variables and canonical axes. A Monte Carlo permutation test using the default number of permutations (199) was used to test the significance of the canonical axes. Biplots of species and quadrats with environmental gradients were displayed to show the correlation obtained from the multivariate analyses using CANODRAW (ter Braak & Šmilauer 1998; Šmilauer 1992).

Before running analyses in CCA, the species data were square root transformed and high abundances were down-weighted to maximize the dispersion of species. Soil fertility data were log-transformed because small differences in nutrient concentration are more important at lower concentrations than at higher concentrations (Palmer 1993). Finally, aspect data were transformed by trigonometric functions (northness (north aspect) = cos (aspect); eastness (east aspect) = sin (aspect)) because these data are circular.

Results

In this study, 73 quadrats were sampled and 159 species encountered. Of these, 35 were grass species, 106 forb species and 18 woody species. The number of species per quadrat ranged from 10 to 50 with an average of 28 species per quadrat. The species with the highest relative quadrat frequency at Black Mesa were Opuntia phaeacantha (94%), Opuntia imbricaria (87%), Bouteloua curtipendula (83%) and Bouteloua gracilis (82%). The average species cover per quadrat ranged 0.01 to 16.3 percent cover, Bouteloua gracilis (16.3%) and Bouteloua curtipendula (11%) scoring the highest average cover.

Over the entire 30-month period, north and south facing slopes recorded 20% less annual rainfall while the top recorded 25% less annual rainfall when compared with the northern and southern base sites. Regarding temperature, the north and south base sites were similar, with the top 0.5°C cooler. Overall, no significant differences were statistically encountered.

The quantitative analyses and the main explanatory gradients between the DCA and CCA ordinations were similar. A diagram of the DCA site ordination is shown in Figure 4a. Eigenvalues for axes I and II were 0.545 and 0.276, respectively and explained 82.1% of the species data. The correlation analysis between the DCA axis scores and the environmental data showed that axis I represented a topographic and geomorphic gradient increasing in slope ($r=0.8205$, $p=0.05$), rock cover ($r=0.7575$, $p=0.05$), large rock size ($r=0.6592$, $p=0.05$) and sand content ($r=0.5874$, $p=0.05$) (Table 1). Axis II represented decreasing nutrient availability (phosphorus: $r=-0.6083$, $p=0.05$; potassium: $r=-0.5924$, $p=0.05$; nitrogen: $r=-0.5173$, $p=0.05$).

Qualitatively, there were two underlying floristic gradients that could be interpreted from the DCA ordination. Axis I represented a short grass to tall grass gradient as well as a grassland to Rhus aromatica dominated shrubland gradient. Although axis II was more difficult to interpret because of small eigenvalues, it may represent a shrubland to Juniperus monosperma dominated woodland.

Eigenvalues for axes I and II from the CCA ordination were 0.341 and 0.163, respectively and explained 50.4% of the variance in the weighted averages of species with respect to the environmental variables (Figure 4b). The species environment correlations, measuring the strength of the relation between the species and the environment for the first two axes, were 0.961 and 0.903, respectively. The first two axes accounted for 29.9% and 14.4% of variance in the weighted average of the species with respect to the environmental variables. CCA axis I described a strong topographic and geomorphic gradient where steeper slopes were positively correlated with increased rock cover dominated by larger rocks and sandier soils.

The first CCA axis defined the strongest gradient, which was significantly correlated with slope ($r=0.8295$, $p=0.05$) (Table 1). CCA axis I was also strongly correlated with the largest rock class (S7; $r=0.7411$, $p=0.05$) and to a lesser degree with rock cover ($r=0.6864$, $p=0.05$) and sand content ($r=0.5757$, $p=0.05$). Soil depth was negatively correlated with these gradients. CCA axis II was correlated with potassium ($r=0.7077$, $p=0.05$) and phosphorus ($r=0.7014$, $p=0.05$) and represents a nutrient gradient. CCA axes III and IV were not analyzed because of their low canonical eigenvalues 0.122 and 0.093, respectively.

Relationships between the environmental variables were directly related to their distribution in ordination space (Figure 5).

The Monte Carlo permutation tests indicated that both the overall effect of the environmental variables on species data, as well as the first canonical axis, were significant at the 99.5% level ($p<0.0050$). The result of the marginal forward selection, which tests the explanatory power of each environmental variable separately, shows that slope has the highest explanatory power (26%). Slope was followed by rock cover (22%) and the largest rock size (S7; 20%), the same variables that were correlated with CCA axis I. Other important variables were pH (18%), nitrogen (17%), phosphorus (16%) and sand (16%). Since CCA axis II was not as strongly correlated with an environmental variable as CCA axis I, the rank order of the explanatory variables in the forward selection did not correspond exactly to CCA axis II.

The overall pattern of species richness and diversity occurred approximately in the middle of ordination space (Figures 6a and 6b). Sites with high species richness and diversity were located in areas with moderate rock cover, slope, large rocks and nutrients. Sites with high species diversity were located on the upper slopes near the rim. These sites were more topographically complex and dominated by Rhus aromatica. These sites contained larger sized rocks with increased slopes, sand content and nutrient availability. Other sites with high species diversity occurred on top near the rim and on mid elevation talus slopes dominated by the presence of Juniperus monosperma.

Conversely, sites with high species richness were located on the top of Black Mesa and the mid-to-lower slopes. These sites occurred in less

topographically complex areas dominated by Juniperus monosperma. These sites contained small to medium sized rocks with lower slopes and moderate nutrient availability. Results from the correlation matrix showed that species richness, evenness and diversity were not significantly correlated with any of the environmental variables.

Biplots of wood, grass and forb species and environmental gradients are shown in Figures 7, 8 and 9, respectively. Woody vegetation was most associated with environments dominated by the largest rock sizes on the steepest slopes with increased nitrogen in sandy soils. These species included: Brickellia brachyphylla, Brickellia califomica, Celtis recticulata, Cercocarpus montanus, Prunus virginiana, Ptelea trifolata, Rhus aromatica, Ribes cereum, Sapindus saponaria and Toxicodendron radicans (Figure 7). Juniperus monosperma and Mimosa borealis were typically found on northern slopes with increased rock cover and medium-sized rocks. Yucca glauca inhabited areas with slightly higher pH levels, smaller rock sizes and clay-rich soils.

Nitrogen, large rocks and increasing slopes explained the distribution of many grass species (mostly taller species), which coincided with most woody vegetation. These species included: Agropyron smithii, Andropogon gerardii, Andropogon saccaroides, Bouteloua eripoda, Bromus tectorum, Chloris verticillata, Digitaria cognata, Elymus canadensis, Eragrosits spetabilis, Panicum obtusum, Panicum virgatum, Poa fenleriana, Setaria leuchopila, Sorghastrum nutans, Tridens muticas (Figure 8). Lycurus pheloides, Schizachyrium scoparium and Stipa comata were found in areas dominated by increased rock cover and medium-sized rocks. Smaller rock sizes and increased silt, clay and

soil depth coincided with the distribution of the shorter grass species. These species included: Arisitda oligantha, Aristida purpurea, Bouteloua gracilis, Buchloë dactyloides, Hilaria jamesii and Muhlenbergia torreyi.

The distribution of forbs at Black Mesa was similar to the distribution of grass species as described by the nitrogen gradient, but otherwise, the general distribution was distributed across all gradients (Figure 9). When compared to the distribution of woody species, the spatial distribution of forbs was the exact opposite. Carex gravida, Cheilanthes lanosa, Croton gladulosus, Galium texense, Lappula redowski, Lepidium densiflorum, Senecio plattensis and Vitus vulpina were found in environments dominated by large rocks, increased slope and high amounts of nitrogen and phoshorus. Onosmodium molle was found in sandy soils dominated by steep slopes and large rocks. Dalea candidum, Dalea tenufolia, Erigrostis jamesii, Ipomoea leptophylla, Lesquerella ovalifolia, Tradescantia occidentalis inhabited areas with increased rock cover and smaller rocks.

Figure 10 shows the species with the highest species abundance in ordination space. Bouteloua gracilis, the most abundant species at Black Mesa, was associated with other short grasses (Arisitda oligantha, Aristida purpurea, Buchloë dactyloides and Hilaria jamesii) and gradients that represent grassland areas. Bouteloua curtipendula, the second most abundant species was found at the center of the ordination biplot, located in grassland and shrubland environments. The majority of the abundant species occurred in areas with increased slope, larger rock sizes and more available nutrients. Woody species (Artemesia ludoviciana, Celtis recticulata, Ptelea trifolata, Rhus aromatica and

Sapindus saponaria) and taller grass species (Agropyron smithii, Andropogon gerardii, Andropogon saccaroides, Panicum obtusum, Poa fenleriana and Tridens muticas) mostly occurred in shrubland or mixed grassland/shrubland environments. Bouteloua eriopoda was the only short grass that occurred under these site conditions.

Discussion

Although the most important climatic factors that affect the structure and composition of species at larger scales in semi-arid environments are temperature and precipitation (Noy-Meir 1973), the use of direct and indirect gradient analysis showed that species structure and composition of vegetation at smaller scales were most affected by topography and geomorphology (slope, rock size, rock cover and sand content) and nutrient availability (nitrogen, phosphorus, potassium). Despite the significance of climate at broader scales (Cox & Larson 1992; Duckworth et al. 2000), temperature and precipitation at Black Mesa was not shown to be a major factor affecting the distribution of vegetation at the scale of analysis defined by this study. Of the relationships observed in temperature and precipitation, the affect of elevation and wind, respectively, could account for such differences. Although the variation in precipitation was not significant at Black Mesa, local topo-edaphic factors affect water and nutrient availability, which ultimately affects the structure and composition of vegetation (Weins 1976). At Black Mesa, the majority of the structure and composition of vegetation was explained by axis I in both ordination diagrams (Figures 4a and 4b).

At a much larger scale, if the climatic variables at Black Mesa were compared with the rest the Mesa de Maya or portions of the Great Plains, they might be more significant as larger scale gradients. For example, climatic variables may best explain the disjunct distributions of Pinus edulis and Pinus ponderosa at Black Mesa, two species found in abundance further to the west.

On the other hand, the importance of local site factors affecting the structure and composition of vegetation at Black Mesa agree with Neilson et al. (1992). They state that areas where climate is more stressful for plant life (extreme cold, heat or dryness), species are more likely to respond to smaller scale variations in substrate, topography and biotic interactions than climatic factors.

Likewise, Ohmann and Spies (1998) showed that as species variation explained by climate decreased, variation explained by local factors increased with decreasing geographic extent. The analysis presented here showed that species variation at Black Mesa was best explained by site level topo-edaphic factors rather than larger scale (in relation to the other factors) climate variables. Although not measured extensively in this study due to cost and accessibility, micro-climatic effects at each site are probably associated with local site conditions and important to the structure and composition of vegetation.

Similar to Black Mesa, other studies have found that local topo-edaphic factors explain the distribution of vegetation. Parker (1991) demonstrated that coarser soils related to the weathering of granite increased frequency of three cacti species, Carnegiea gigantea, Lophocereus schottii and Opuntia fulgida and finer soils related to basaltic weathering contained greater distributions of shrubs, Ambrosia dumosa and Larrea tridentata. McAuliffe (1994) showed that the distribution of Larrea tridentata was explained by the age of geomorphic substrate (Holocene deposits) and soil texture (non-argillic horizons). Similarly, Black Mesa's unique geologic history and formation directly affect the distribution of vegetation communities through its spatially complex topography.

Patterns of species richness and diversity revealed that environments with the greatest species richness and diversity occurred in the middle of ordination space (Figures 6a and 6b) and agreed with hypotheses linking maximum species coexistence to moderate habitat structure (Schluter & Ricklefs 1993; Tilman & Pacala 1993). Habitat structure, as defined in terms of landscape ecology, is the distribution of energy, materials and species (Forman and Godron 1986; Turner 1987; Risser 1990; Forman 1995). The degree of habitat structure is related to the unequal distribution of energy, materials and species where vegetation structure and composition is determined by the differential responses of species to abiotic and biotic conditions (Austin 1985; Huston 1979; Whittaker 1967; Gleason 1926). As a result, environments with greater habitat structure and unequal distribution of resources tend to contain greater species richness and diversity (Forman and Godron 1986; Rosenzweig 1995).

For example, Montaña (1990) showed that the greatest species richness and diversity in the southern Chihuahuan Desert was linked to moderate habitat structure defined by rockiness, topography and soil texture. Rosenzweig & Ambramsky (1993) demonstrated that moderate habitat structure occurred at intermediate levels of productivities, usually measured by intermediate levels of biomass (Grime 1973, 1979; Al-Mufti et al. 1977; Tilman 1982, 1997). Therefore, increased productivity (increasing the supply rate of a limiting resource) leads to increased competitive exclusion and a decrease in species richness and diversity whereas intermediate productivity moderates competitive exclusion and produces species rich and diverse habitats (Tilman 1986; 1982; Huston 1979). At Black Mesa, the greatest species richness and diversity was found in areas

with moderate habitat structure containing a mixture of shrubland and grassland species. These environments contained medium sized rocks, moderate slopes and moderate amounts of surface rock cover and nutrients (Figures 6a and 6b).

In terms of species competition, habitats with little structure contain superior competitors that eliminate inferior competitors whereas highly structured habitats contain more dominant or colonizing species that reduce existing competitors. As a result, a balance between competitors and colonizers in moderately complex habitats affords the best opportunity for increased species richness and diversity (Grime 1979). Tilman (1982) noted that areas with high species diversity (and low species richness) were found in highly structured habitats, where colonizers have established specific resource needs under extreme competition (Tilman 1982).

For example, competitive exclusion by the shrub Larrea tridentata decreased species richness on bajadas in the northeastern part of the Sonoran Desert (McAuliffe 1994). These sites contained high surface rock cover, large rocks, steeper slopes and coarse textured soils, resulting in high species diversity. Similarly, at Black Mesa, sites dominated by Rhus aromatica were located in areas of steep slopes, large rocks, higher nutrient availability, coarse-textured soils and high species diversity (Figures 6a and 6b). Sites with high species richness (and low species diversity) were found in areas with lower habitat structure and nutrient availability. Although there were slight differences between environments with high species richness and high species richness and diversity, species rich sites contained more grassland species, which increased the number of forb species and increased species richness.

The abundance of woody and tall grass species was mostly influenced by the presence of large rocks, increased slopes and higher nutrient availability. The source of rocky material and increased slope at Black Mesa is a product of geologic history and differential erosion (Rothrock 1925; Stovall 1943; Suneson & Luza 1999). The source of basaltic rock cover at higher elevations is the rim of the Mesa while sandstone blocks at lower elevations originate from the various geologic seams that are visible on the slopes. The highest densities of rocks occur near the basaltic rim and sandstone outcrops, talus slopes and drainage and canyon areas.

At Black Mesa and other similar environments, larger rocks and coarser soils settle closest to the source and smaller rocks and finer soils settle farther down slope. The larger rocks and coarser soils allow more rapid infiltration of water and higher water potentials than smaller rocks and finer textured soils, thus making more plant-available soil moisture and nutrients for species to survive in dry environments (Yang & Lowe 1956; Key et al. 1984; Bowers & Lowe 1986). The relationship between larger rocks, coarser soils, increased soil moisture and nutrients are common in semi-arid environments and are best explained by the inverse texture effect (Noy-Meir 1973; Foth 1984; Walter 1985).

The inverse texture effect states that fine-textured soils in semi-arid environments provide less moisture for plant growth because when precipitation enters the upper soil profile and is held by higher water-holding capacities, the moisture is more readily lost by evaporation than the same precipitation that penetrates deeper in coarser-textured soils with lower water-holding capacities. For instance, Parker (1991) discovered steep rocky upland areas; coarse-

textured soils and high levels of magnesium were dominated by woody species Ambrosia dumosa and Larrea tridentata. These sites exhibited higher soil-moisture and nutrient availability. Similarly, McAuliffe (1994) discovered similar relationships as Parker (1991) and added that Larrea tridentata was not present on fine-textured soils with high pH. At Black Mesa, the most abundant species were indicators for sites that contained larger rocks, steeper slopes, sandier soils and higher nutrient availability (Figure 10). These structurally complex environments contained increased nutrient availability, which might be related to the water availability in coarser-textured soils.

It is widely accepted that herbaceous species obtain moisture at shallower depths and woody species at greater depths (Walter 1971). On the other hand, shallow-rooted woody species (i.e. Juniperus monosperma) or deep-rooted grass species (i.e. Schizachyrium scoparium) will dominate if competitive conditions exist (Schlesinger et al 1990). Many of these conditions are directly related to limiting resources (Tilman 1982) and niches (Austin 1985; Hutchinson 1978; Odum 1971), where species tend to separate their niches and reduce resource (biotic and abiotic) competition. A niche in the context of this research refers to the subdivision of the environment occupied by a species under competition with other species (Grinnell 1924).

An innovative way to look at the ordination diagrams is in terms of limiting resources and suitable niches. In this respect, the ordination diagram represents a linear combination of environmental variables that maximally separates the niches of species (ter Braak and Verdonschot 1995). The more limiting the resource, the narrower the niche for a particular species, and the farther the

species is located from the center of the ordination diagram. For example, the spatial pattern of forb species shows a majority of species clustered in the center of ordination space with no specific resource or habitat needs while species farther from the center require specific resource and habitat needs (Figure 9). This is also the case for grass and woody species near the end of the slope, large rock and nitrogen gradients (surrogates for increased water and nutrient resource needs) (Figures.7 and 8).

The ordination diagrams can also be used to represent the relationship between habitats and species (and their associates). For example, in areas with scant distributions of Juniperus monosperma, short and mixed grasses Aristida oligantha, Bouteloua curtipendula, Bouteloua gracilis, Bouteloua hirsuta, Buchloë dactyloides, and Hilaria jamesii dominate. These species represent indicators for increased soil depth, silt, clay, pH levels and smaller rock sizes. The effect of soil texture on the distribution of Bouteloua gracilis and Buchloë dactyloides is also consistent with Coffin and Lauenroth (1994, 1989) and Martinez-Turanzas et al. (1997). In addition, many forbs govern these areas since grass and forb richness is highly correlated at Black Mesa, which agrees with literature on grasslands (French 1979; Sims 1988; Knapp et al. 1998).

Conclusions

Multivariate analysis was used to explore environmental factors affecting vegetation structure and composition, as well as patterns of species richness and diversity, in a semi-arid mesa environment. Analyses showed that vegetation structure and composition were most affected by topography and geomorphology (slope, rock size, rock cover and sand content) and nutrient availability (nitrogen, phosphorus, potassium). Furthermore, This research suggests that the primary factors affecting the structure and composition of vegetation were related to two limiting factors: moisture availability (as expressed by slope, rock cover, rock size and soil texture) and soil nutrients (explained by nitrogen, phosphorus and potassium and controlled by slope, rock cover, rock size and soil texture). Although this research focused on predetermined environmental gradients, other gradients that might explain additional variance in species-environment relationships could be related to soil moisture (Witkowski & O'Connor 1996), bulk density (San Jose et al. 1998), heat index and solar radiation (Parker 1991) or evapotranspiration (Currie & Paquin 1987).

The greatest species richness and diversity was found in areas with moderate habitat structure containing a mixture of shrubland and grassland species. These environments contained medium sized rocks, moderate slopes and moderate amounts of surface rock cover and nutrients. Increased habitat structure resulted in higher species diversity and decreasing habitat structure resulted in higher species richness. In addition, the abundance of woody and tall grass species was mostly influenced by the presence of large rocks, increased slopes and soil texture and higher nutrient availability. The abundance of shorter

and mixed grass species was mostly influenced by increased rock cover, soil depth and pH, finer textured soils and decreased rock size. These relationships were closely connected with the inverse texture effect, limiting resources and niches and were important for better understanding species structure and composition.

In comparing constrained (CCA) and unconstrained (DCA) ordination, it was determined that both techniques increased the effectiveness in quantifying patterns of species structure and composition related to the environment. According to McGarigal et al. (2000), if both analyses produce "similar" results, then the measured environmental variables account for most of the variation in the species composition. Visually, both ordination diagrams showed similar distributions of species and sites. Likewise, the correlation between ordination axis scores and environmental variables produced similar results. In addition, the sum of the first two eigenvalues for the DCA and CCA were 0.82 and 0.50, respectively. According to McGarigal et al (2000), when CCA explains less variance than DCA, and the CCA species-environment correlation is high (0.961 and 0.903 for axis I and II, respectively) then the measured environmental variables are significant, even though other factors may be important.

On the other hand, other factors may not exist since the assumptions for canonical ordination are rarely met (i.e. samples are random and environmental variables are constant throughout). Another disadvantage of canonical ordination is that one must prejudge which environmental factors are important to the distribution and composition of vegetation (Beals 1984) where the analyses are restricted by measured environmental variables (McCune 1997). Overall, the

value added by using multivariate analysis has gone beyond quantification of obvious patterns in vegetation structure and composition and moved toward testing hypotheses that relate more to ecological processes and concepts that are useful for interpreting and explaining ordination results.

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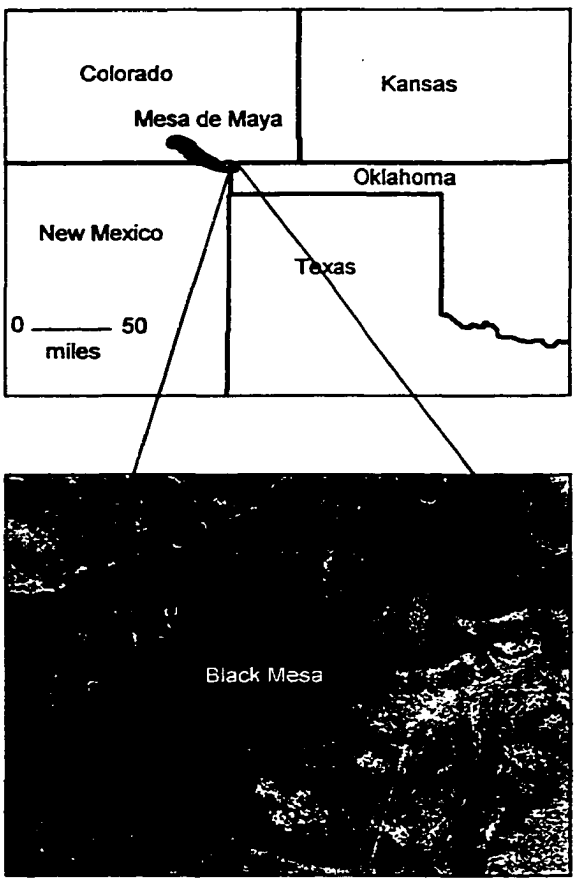
Legend Table 1

Summary of a weighted correlation matrix and corresponding correlation coefficients (r-values) between the environmental variables and the first two DCA and CCA axes. Environmental variables include: species richness [S], species evenness [E] (Pielou 1977), Shannon's diversity index (H'; Shannon and Weaver 1949), soil depth [SD], % slope [SL], north aspect [north], east aspect [east], rock size classes from smallest to largest [S1-S7], total mean rock cover [TMRC], elevation [EL], soil pH [PH], nitrogen [NO_3], phosphorus [P], potassium [K], % sand [SAND], % silt [SILT] and % clay [CLAY]. Axis I in both ordinations represent a topographic / geomorphic gradient (correlated with slope, larger rock sizes and rock cover) and axis II represents a nutrient gradient (correlated with nitrogen, phosphorus and potassium).

Variable	DCA Correlation Coefficient		CCA Correlation Coefficient	
	Axis I	Axis II	Axis I	Axis II
S	-0.07	-0.0902	-0.1455	0.0235
E	0.6972	-0.3103	0.5571	0.1432
H'	0.4408	-0.3006	0.3455	0.1139
SD	-0.5869	0.1515	-0.5764	-0.051
SL	0.8205	-0.1449	0.8295	0.0742
NORTH	X	X	0.0514	0.2287
EAST	X	X	-0.2127	-0.1372
S1	-0.7111	0.2824	-0.5394	-0.1026
S2	-0.3355	0.3084	-0.5176	0.1057
S3	0.2434	0.0784	0.102	0.323
S4	0.2762	-0.1336	0.1473	-0.0045
S5	0.4191	-0.1301	0.2891	0.0357
S6	0.5489	-0.1619	0.5036	0.0189
S7	0.6592	-0.2773	0.7411	-0.0973
TMRC	0.7575	0.0682	0.6864	0.4975
EL	-0.5395	-0.1067	-0.329	-0.3181
PH	-0.5021	0.3633	-0.6507	0.2397
NO_3	0.3494	-0.5173	0.5933	-0.4365
P	0.1899	-0.6083	0.438	-0.7014
K	-0.0923	-0.5924	0.0919	-0.7072
SAND	0.5874	0.0531	0.5757	0.1884
SILT	-0.3866	-0.1757	-0.43	-0.2939
CLAY	-0.561	0.2104	-0.5428	0.0603

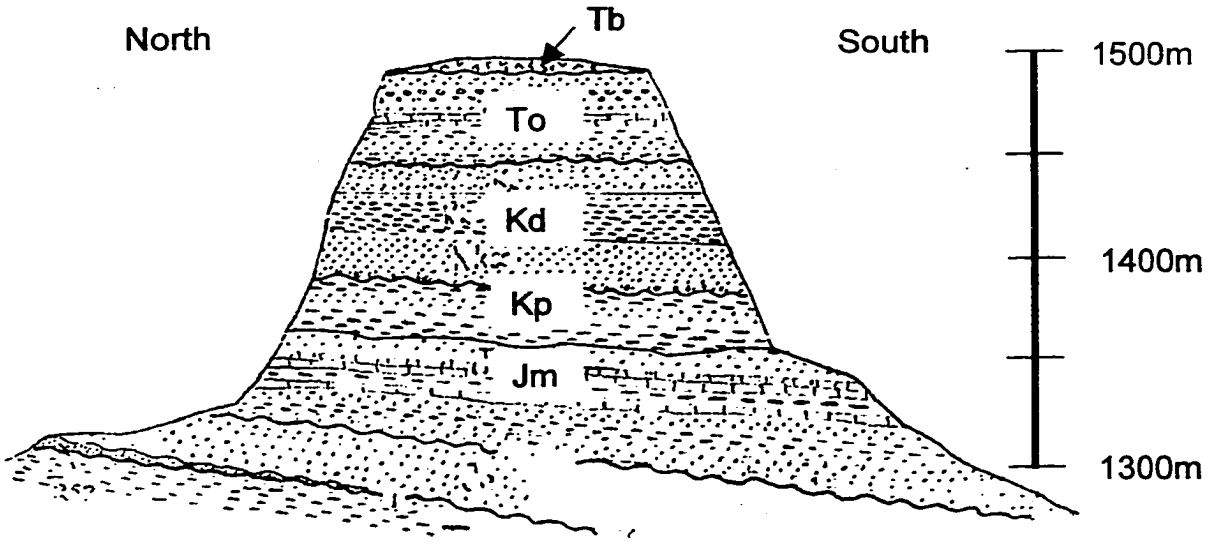
Legend Figure 1

Study Area. The Mesa de Maya is a lava-capped plateau approximately 72km in length and from 600 to 10km wide. It extends from southeastern Colorado through the northeastern corner of New Mexico and into the northwestern tip of the Oklahoma Panhandle. Most of the plateau lies in Colorado and New Mexico, where it is called Mesa de Maya, while the easternmost lobe, which extends 5 km into Cimarron County, Oklahoma, is known as Black Mesa. This study was conducted in an area of about 18 sq km and includes Black Mesa and its surrounding landscape.


Colorado
Kansas
Mesa de Maya
Oklahoma
New Mexico
Texas
0 ——— 50
miles
Black Mesa

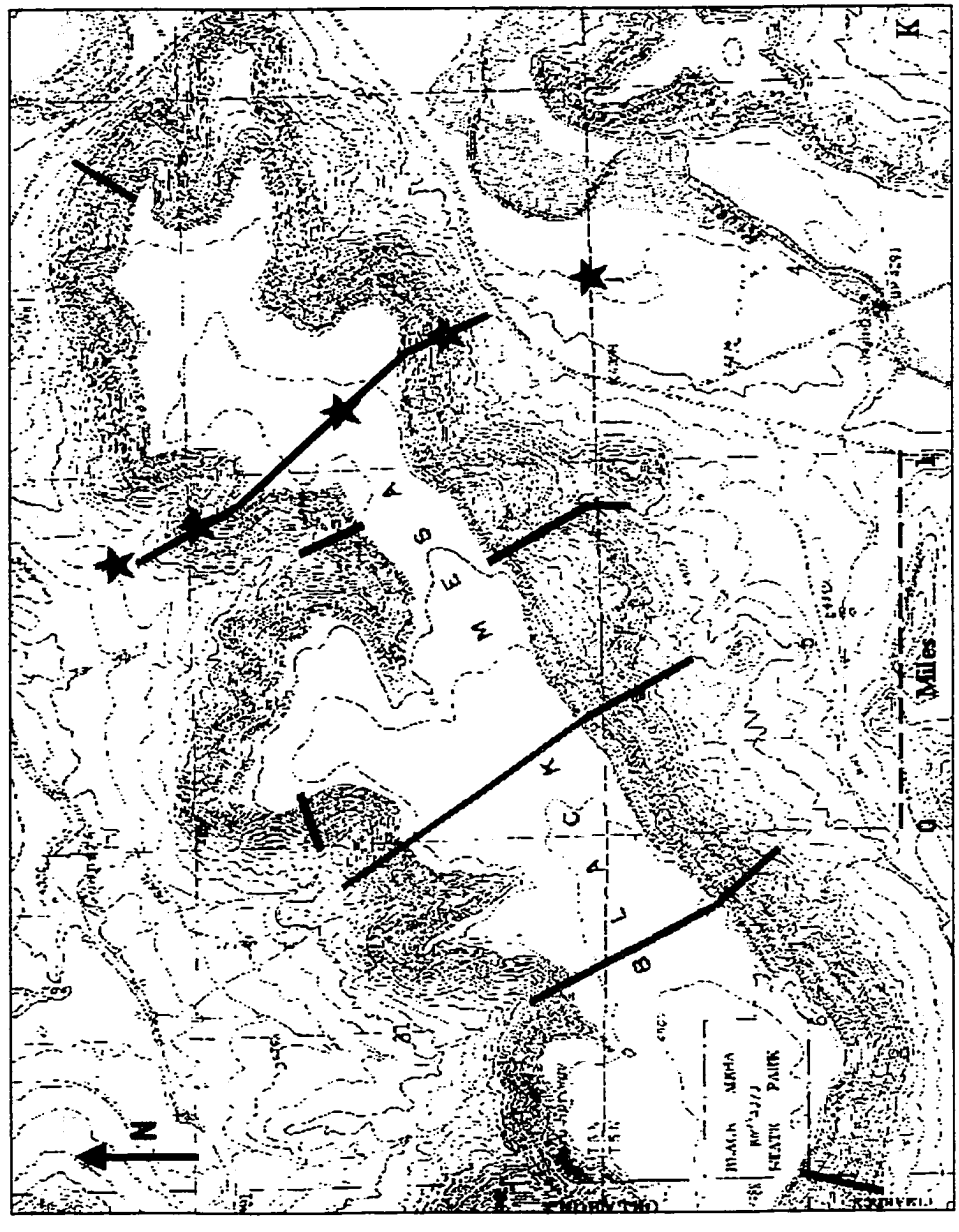
Legend Figure 2

The geologic stratigraphy of Black Mesa, from higher to lower elevation consists of: Raton Basalt (Tb), Ogallala Formation (To), Dakota Formation (Kd), Purgatoire Formation (Kp) and the Morrison Formation (Jm)


North
Tb
South
1500m
To
Kd
1400m
Kp
Jm
1300m

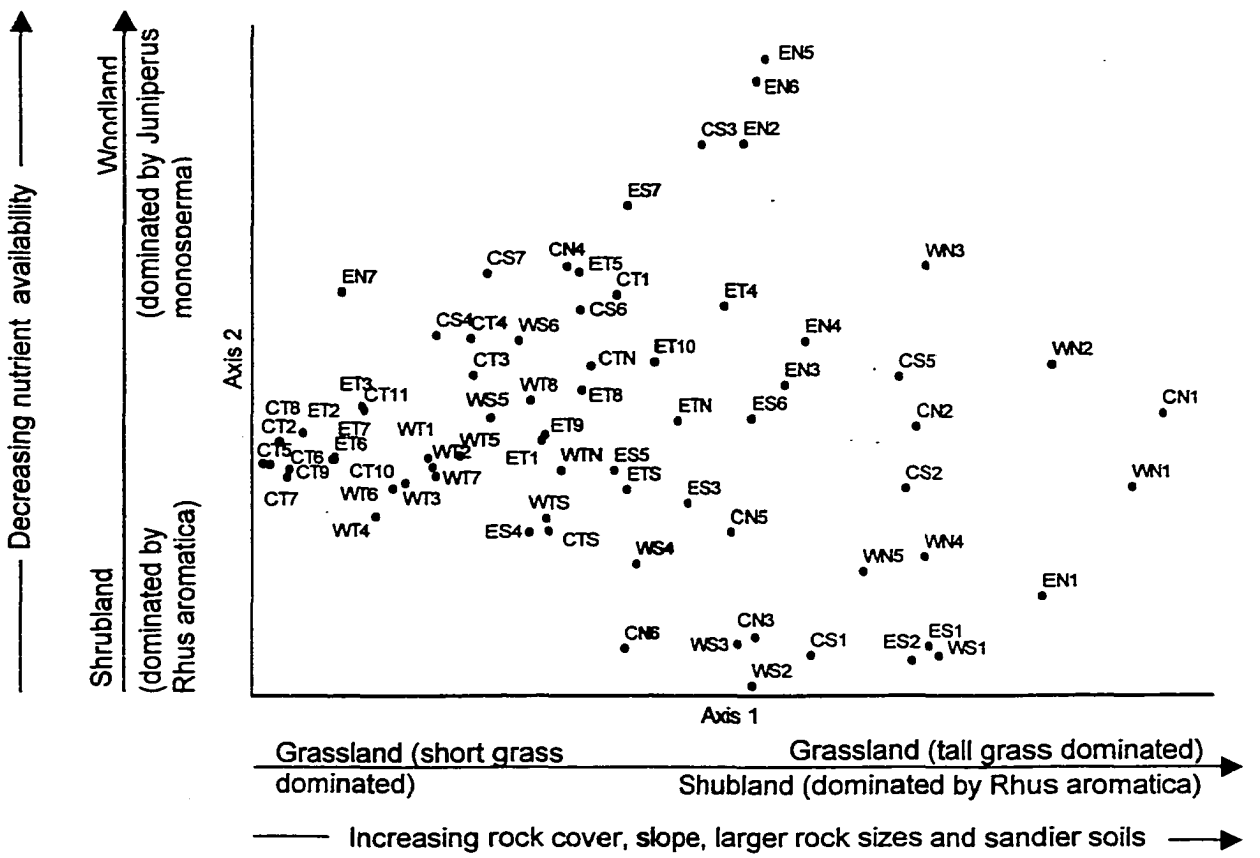
Legend Figure 3

Location of permanent and temporary transects and meteorological stations on a portion of the Kenton USGS 1:24000 Quadrangle. Vegetation data were collected from three permanent transects traversing Black Mesa. Each transect was spaced approximately one mile apart and oriented approximately perpendicular to contour lines. These transects were designated as east, central and west and were composed of 26, 26 and 21 quadrats respectively (blue lines). Each quadrat measured 10 x 10 meters and was placed at 75 meter intervals along the transect. In order to increase the sample size, five additional temporary transects totaling 28 quadrats were located on the slopes in spatially complex areas (short black lines). In order to evaluate the effects of temperature and precipitation at Black Mesa, a total of five meteorological stations were established along the east transect (red stars). One station was located on the top and center of Black Mesa and two stations (one on each side of Black Mesa) were located several hundred meters from its base. These stations collected temperature and precipitation. The horizontal distance between the northern and southern base stations is approximately 2.5 kilometers. Two additional stations, collecting precipitation, were located on the northern and southern slopes of Black Mesa, halfway between the base and rim.


N
BLACK MESA
Miles

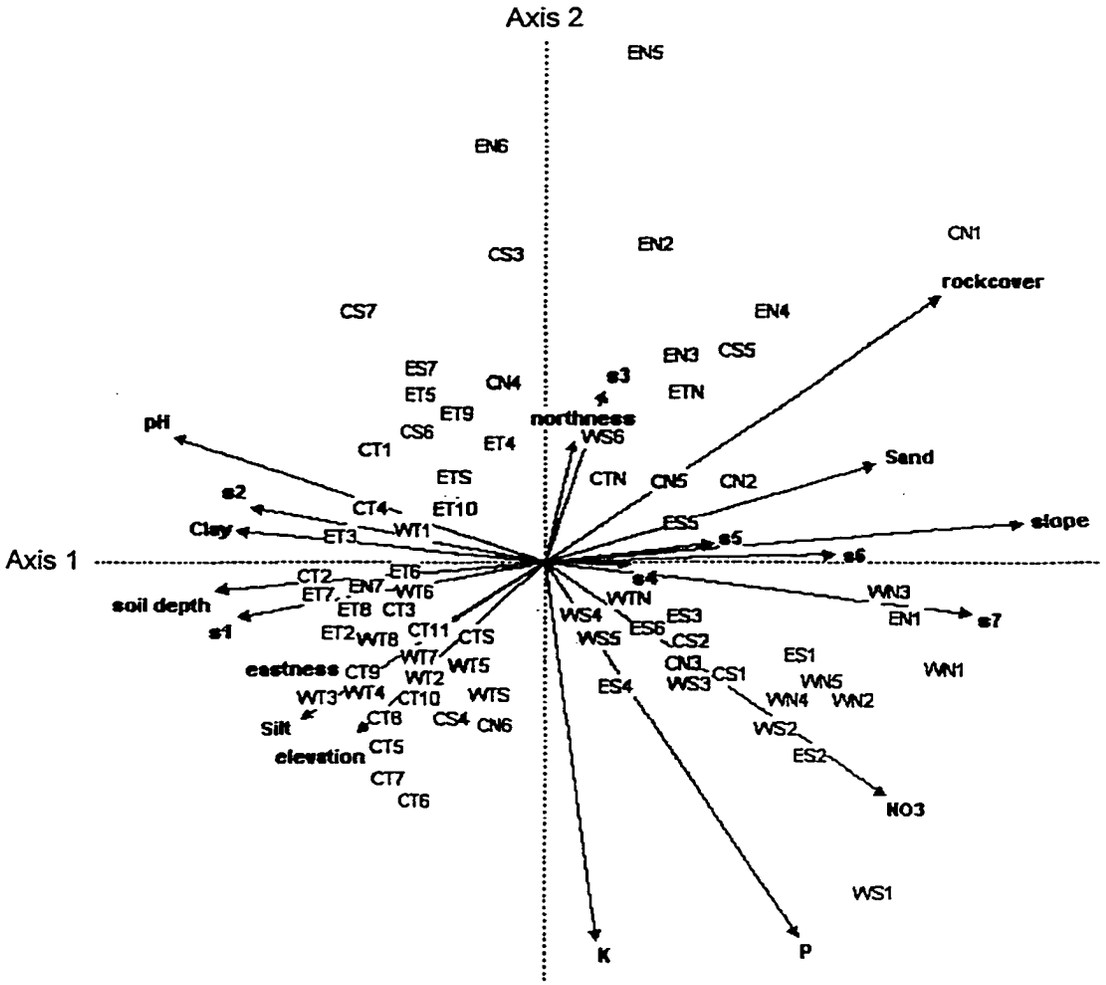
Legend Figure 4a

A diagram of the DCA site ordination. Eigenvalues for axes I and II are 0.545 and 0.276, respectively. Axis I represents a topography / geomorphology gradient and axis II represents a nutrient gradient. Both axes represent floristic gradients. (The first letter represents east "E", central "C" or west "w" transects; the second letter represents south slope "S", north slope "N" or top "T"; the number represents location: "1" near the rim and descending down slope and "1" starts on the north rim on the top and ends at the south rim).


Decreasing nutrient availability
Woodland
(dominated by Juniperus monosperma)
Shrubland
(dominated by Rhus aromatica)
Axis 2
Axis 1
EN5
EN6
CS3 EN2
ES7
CS7
CN4
ET5
WN3
EN7
CT1
ET4
CS6
CS4
CT4
WS6
EN4
WN2
CT3
CTN
ET10
CS5
EN3
ET3
CT11
WS5
WT8
ET8
CN1
CT8 ET2
ETN
ES6
CN2
CT2
ET7
WT1
ET9
ET6
WT5
CT5
CT6
WT2
ET1
WTN
ES5
CT9
CT10
WT7
ETS
CS2
WN1
CT7
WT6
WT3
ES3
WTS
CN5
WT4
ES4
CTS
WS4
WN5
WN4
EN1
CN3
CN6
WS3
CS1
ES2
ES1
WS1
WS2
Grassland (short grass dominated)
Grassland (tall grass dominated)
Shubland (dominated by Rhus aromatica)
Increasing rock cover, slope, larger rock sizes and sandier soils

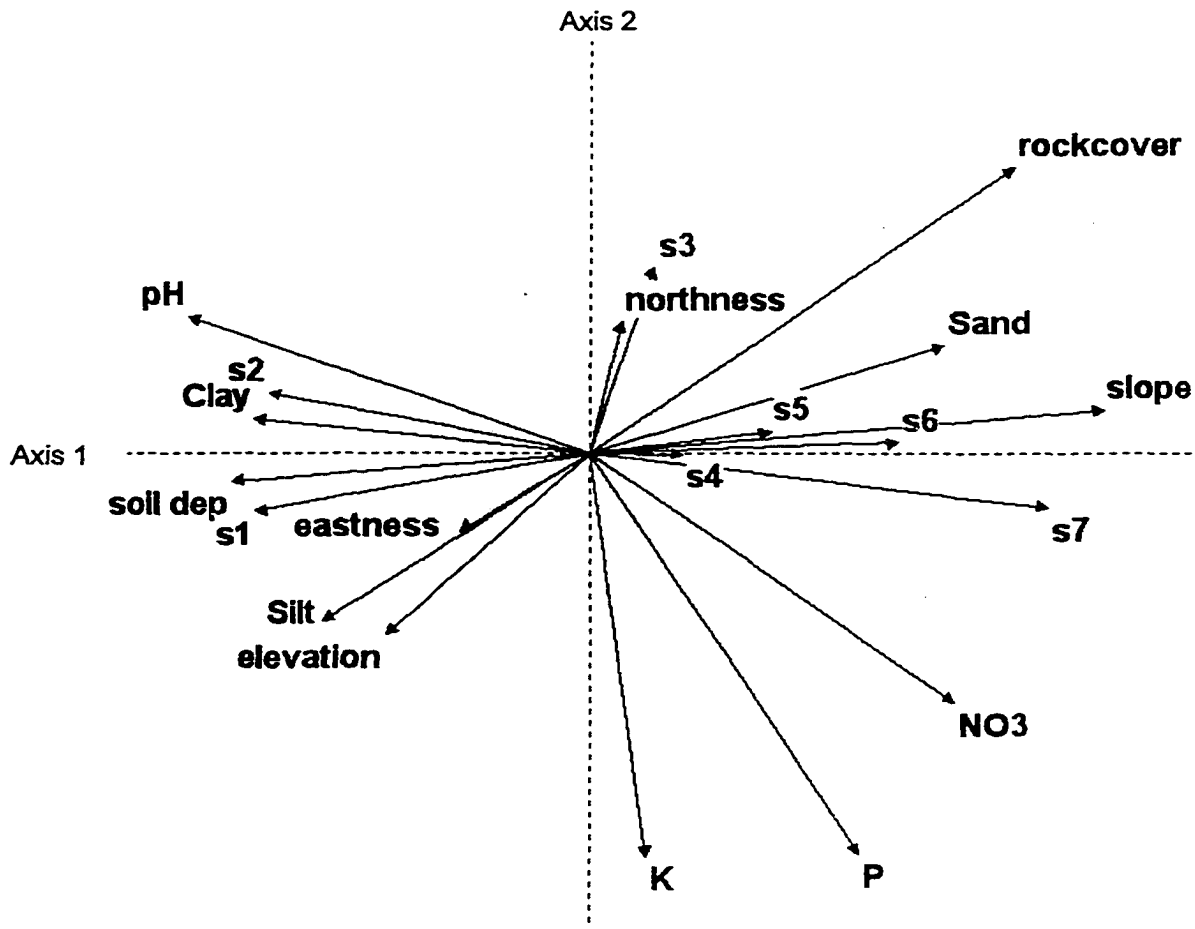
Legend Figure 4b

A CCA biplot of quadrats versus environmental gradients. Eigenvalues for axes I and II are 0.341 and 0.163, respectively. Axis I represents a topography / geomorphology gradient and axis II represents a nutrient gradient. (The first letter represents east "E", central "C" or west "w" transects; the second letter represents south slope "S", north slope "N" or top "T"; the number represents location: "1" near the rim and descending down slope and "1" starts on the north rim on the top and ends at the south rim).


Axis 2
Axis 1
EN5
EN6
CS3
EN2
CN1
rockcover
CS7
EN4
EN3
CS5
ES7
ET5
CN4
s3
ETN
ET9
northness
pH
CS6
WS6
CT1
ET4
Sand
ETS
CTN
CN5
CN2
s2
CT4
ET10
Clay
WT1
ES5
slope
ET3
s5
s6
CT2
ET6
s4
WN3
ET7
EN7
WT6
WTN
soil depth
ET8
CT3
WS4
ES3
EN1
s7
s1
ET2
WT8
CT11
CTS
ES6
WS5
CS2
WT7
ES1
eastness
CT9
WT2
WT5
CN3
WN1
CS1
WS3
WN5
WT3
WT4
CT10
WTS
ES4
WN4
WN2
Silt
CT8
CS4
CN6
WS2
CT5
ES2
elevation
CT7
NO3
CT6
WS1
K
P

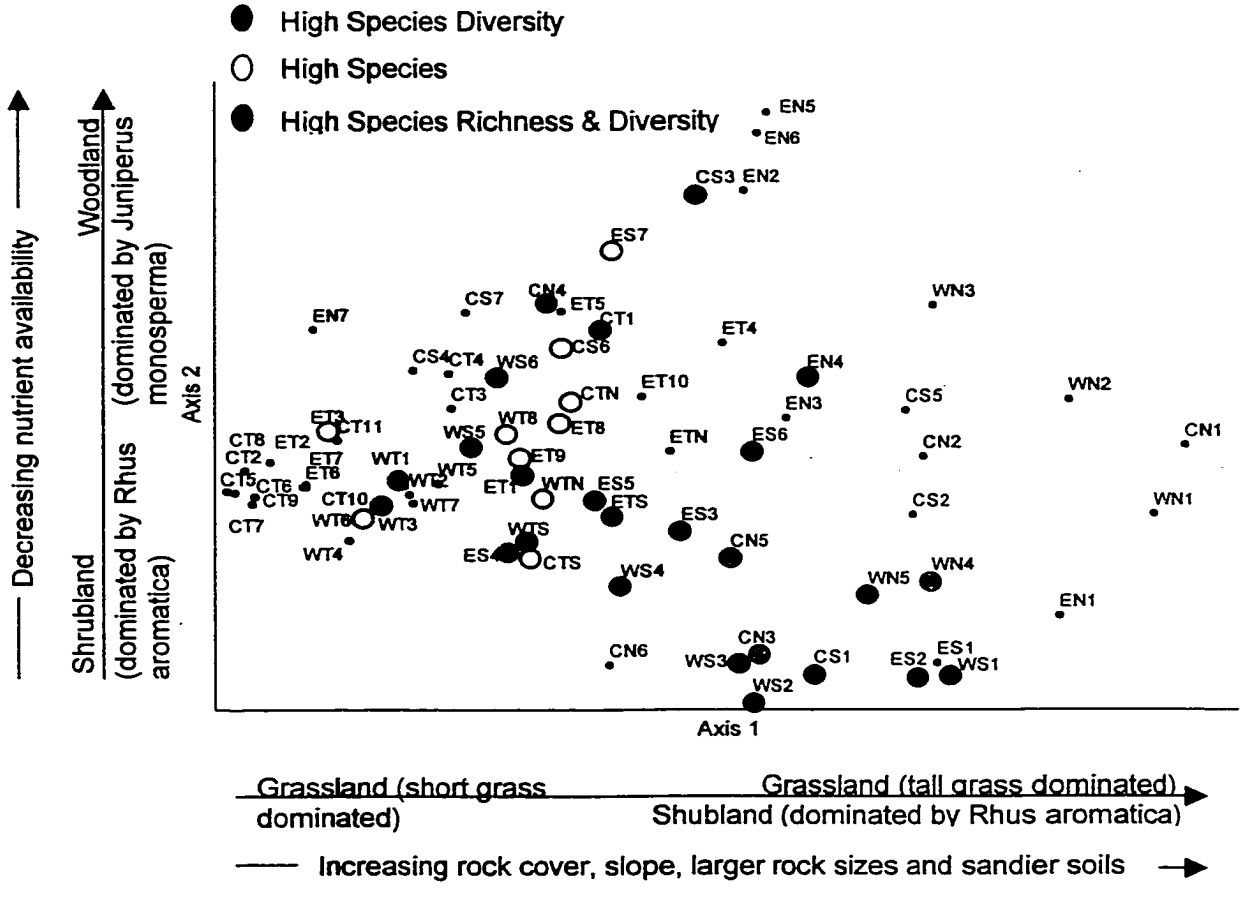
Legend Figure 5

The distribution of environmental gradients in ordination space. Environmental variables with long arrows are more strongly correlated with the ordination axes than those of short arrows. The longer arrows are more closely related to the pattern of community variation. Variables are positively correlated with each other if their arrows form an acute angle and negatively correlated if they form an obtuse angle. The smaller the angle, the stronger the correlation and the larger the angle, the more negative the correlation (ter Braak 1986).


Axis 2
Axis 1
rockcover
s3
northness
pH
Sand
s2
Clay
slope
s5
s6
s4
soil dep
s1
eastness
s7
Silt
elevation
NO3
K
P

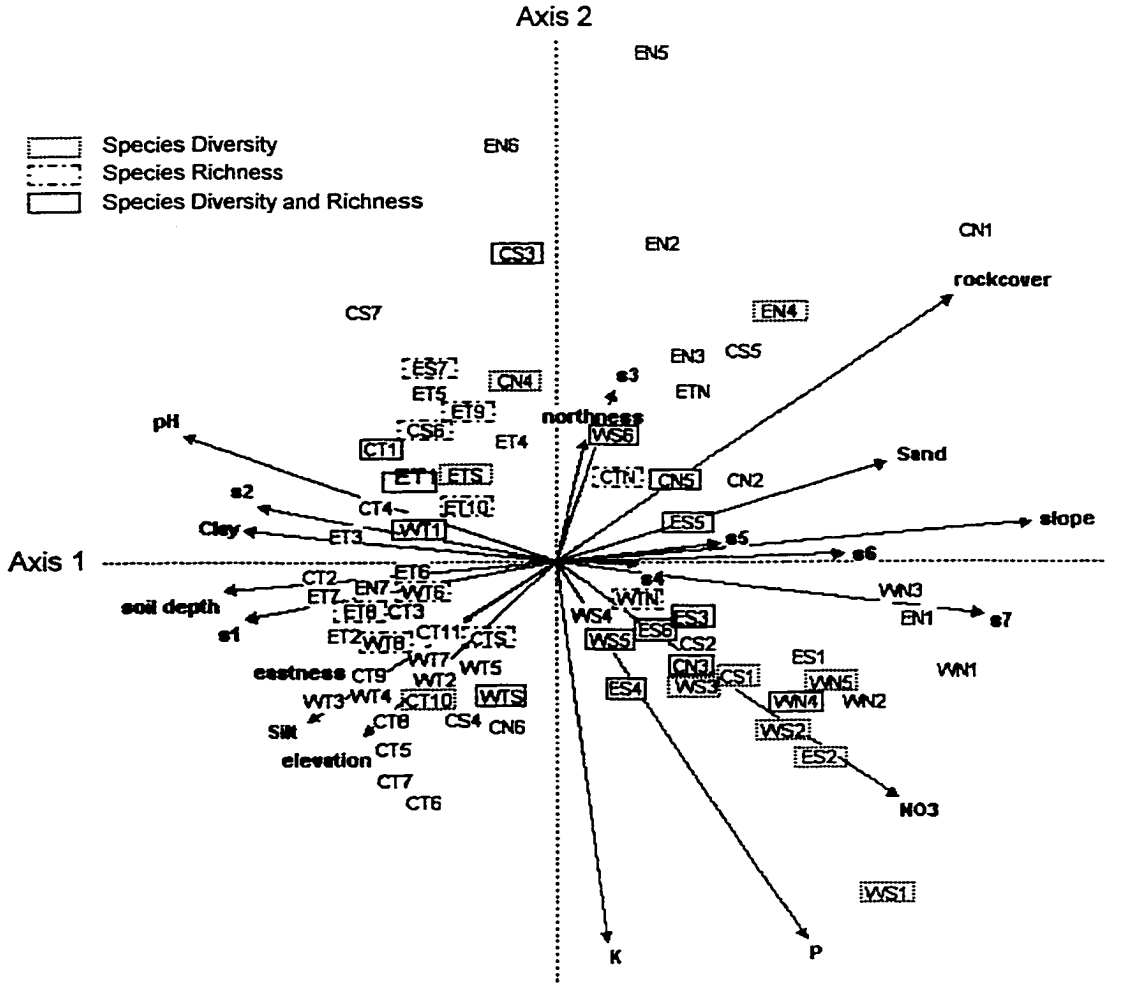
Legend Figure 6a

DCA quadrat ordination showing the location of the 25 greatest species richness and diversity values. Eigenvalues for axes I and II are 0.545 and 0.276, respectively. Axis I represents a topography / geomorphology gradient and axis II represents a nutrient gradient. Both axes represent floristic gradients. (The first letter represents east "E", central "C" or west "w" transects; the second letter represents south slope "S", north slope "N" or top "T"; the number represents location: "1" near the rim and descending down slope and "1" starts on the north rim on the top and ends at the south rim).


High Species Diversity
High Species
High Species Richness & Diversity
Decreasing nutrient availability
Woodland (dominated by Juniperus monosperma)
Shrubland (dominated by Rhus aromatica)
Axis 2
Axis 1
Grassland (short grass dominated)
Grassland (tall grass dominated)
Shubland (dominated by Rhus aromatica)
Increasing rock cover, slope, larger rock sizes and sandier soils
EN5
EN6
CS3 EN2
ES7
CS7
CN4
ET5
CT1
EN7
ET4
WN3
CS4
CT4
WS6
CS6
EN4
CT3
CTN
ET10
CS5
WN2
EN3
ET3
CT11
WT8
ET8
WS5
ETN
ES6
CN2
CN1
CT8
ET2
CT2
ET7
WT1
ET9
WT5
CT5
ET6
CT6
WT2
ET1
WTN
ES5
CS2
WN1
CT9
CT10
WT7
ETS
ES3
CT7
WT6
WT3
WTS
CN5
WT4
ES4
CTS
WS4
WN5
WN4
EN1
CN3
CN6
WS3
CS1
ES2
ES1
WS1
WS2

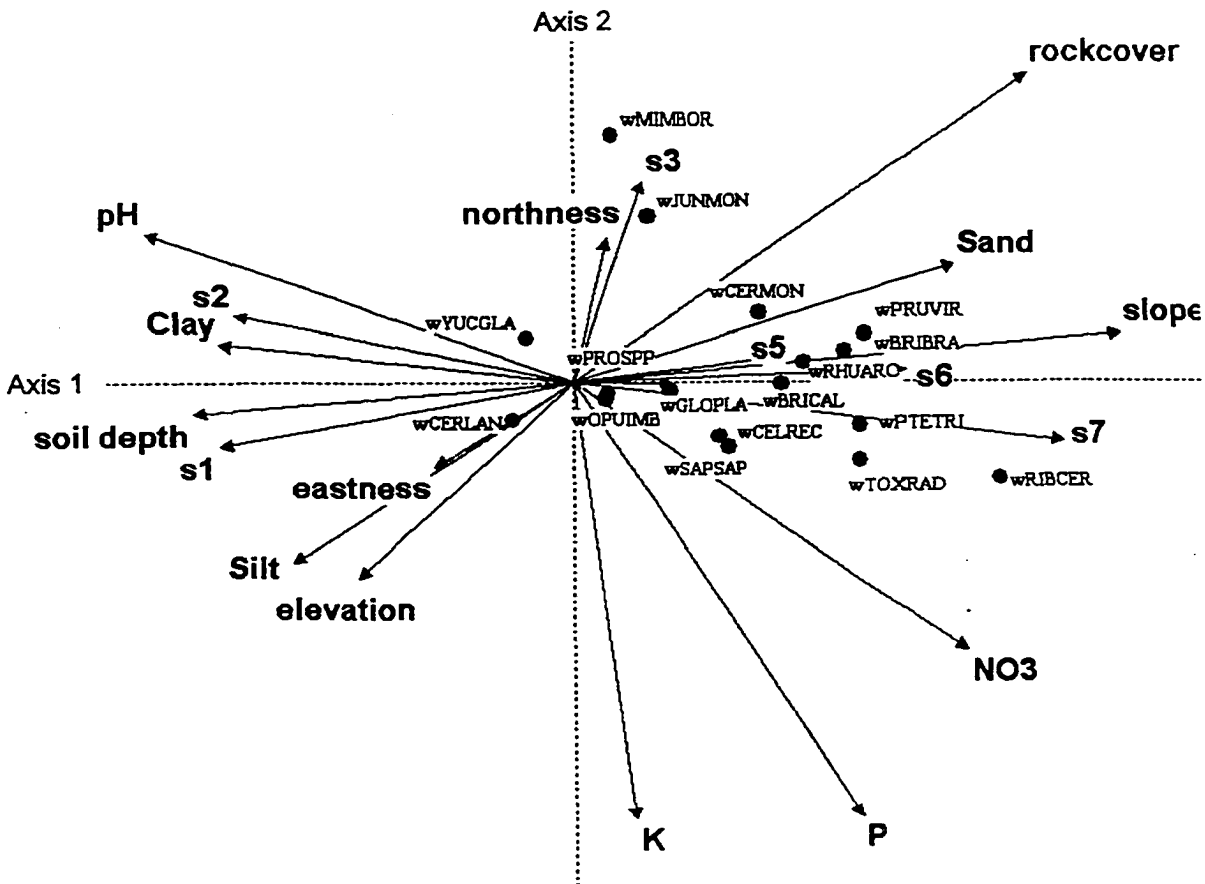
Legend Figure 6b

CCA quadrat ordination showing the location of the 25 greatest species richness and diversity values. Eigenvalues for axes I and II are 0.341 and 0.163, respectively. Axis I represents a topography / geomorphology gradient and axis II represents a nutrient gradient. (The first letter represents east "E", central "C" or west "w" transects; the second letter represents south slope "S", north slope "N" or top "T"; the number represents location: "1" near the rim and descending down slope and "1" starts on the north rim on the top and ends at the south rim).


Axis 2
Axis 1
Species Diversity
Species Richness
Species Diversity and Richness
EN5
EN6
CS3
EN2
CN1
rockcover
CS7
EN4
EN3
CS5
ES7
CN4
s3
ET5
ETN
ET9
northness
pH
CS6
WS6
ET4
CT1
Sand
ET1
ET8
CTN
CN5
CN2
s2
CT4
ET10
ES5
slope
Clay
WT1
ET3
s5
s6
CT2
ET6
s4
ET7
EN7
WT6
WN3
soil depth
WTN
WS4
ES3
EN1
s7
ET8
CT3
ES6
s1
CT11
CT1
WS5
CS2
ET2
WT8
ES1
WT7
WT5
CN3
WN1
eastness
CT9
WT2
CS1
WN5
ES4
WS3
WT3
WT4
CT10
WT8
WN4
WN2
WS2
Silt
CT8
CS4
CN6
CT5
ES2
elevation
CT7
NO3
CT6
WS1
K
P

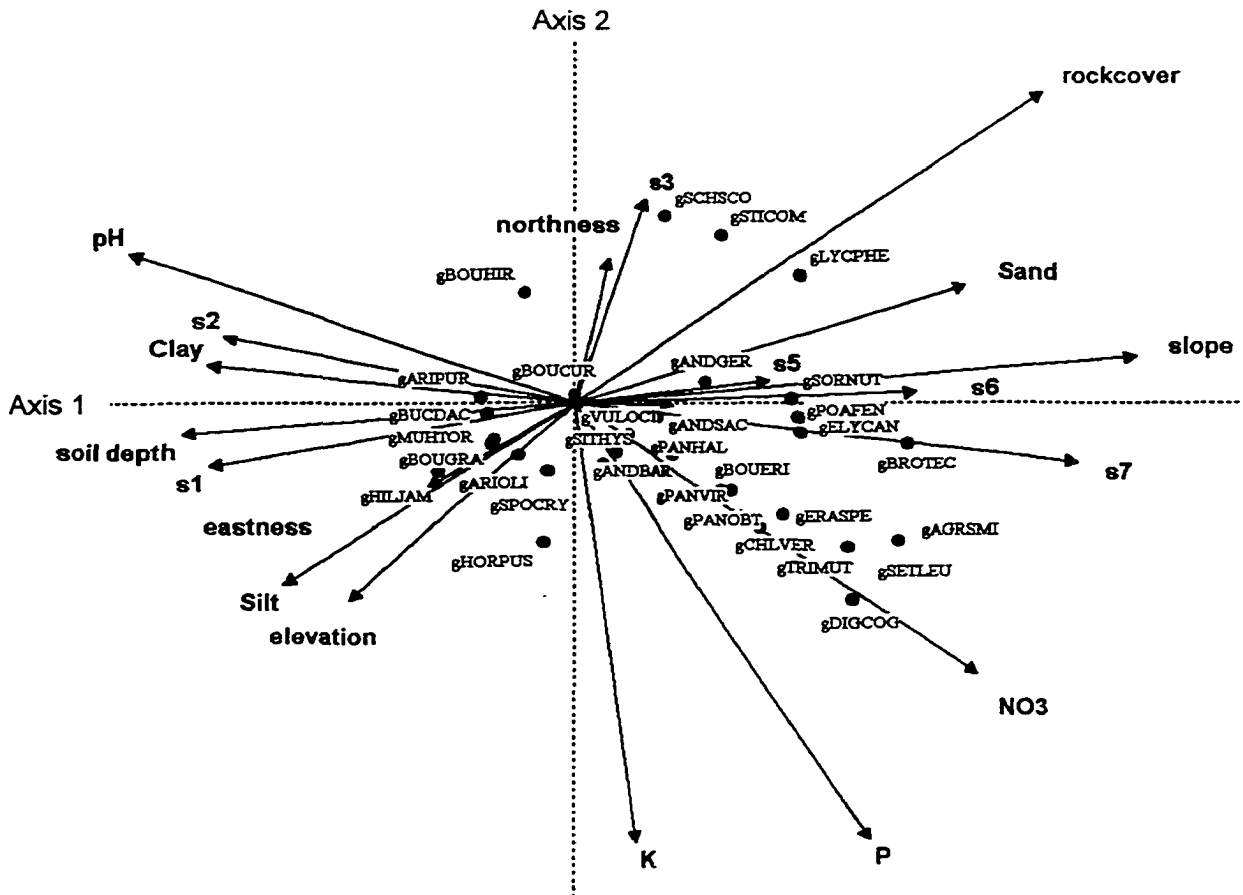
Legend Figure 7

CCA biplot of woody species related to the environmental variables. Woody species are most correlated with large rock sizes, as well as increased slope and sandier soils. The codes represent the first three letters of the two word Latin name preceded by a "w" for woody species. Some of the species include: Brickellia californica (wBRICAL) Brickellia brachyphylla (wBRIBRA), Celtis recticulata (wCELREC), Cercocarpus montanus (wCERMON), Juniperus monosperma (wJUNMON), Ptelea trifolata (wPTETRI), Prunus virginiana (wPRUVIR), Rhus Aromatica (wRHUARO), Ribes cereum (wRIBCER), Sapindus saponaria (wSAPSAP) and Toxicodendron radicans (wTOXRAD).


Axis 2
rockcover
wMIMBOR
s3
wJUNMON
northness
pH
Sand
wCERMON
s2
Clay
wYUCGLA
wPRUVIR
slope
wBRIBRA
s5
wPROSPP
wRHUARO
Axis 1
s6
wGLOPLA
wBRICAL
wCERLAN
wOPUIMB
wPTETRI
s7
soil depth
wCELREC
s1
wSAPSAP
wTOXRAD
wRIBCER
eastness
Silt
elevation
NO3
K
P

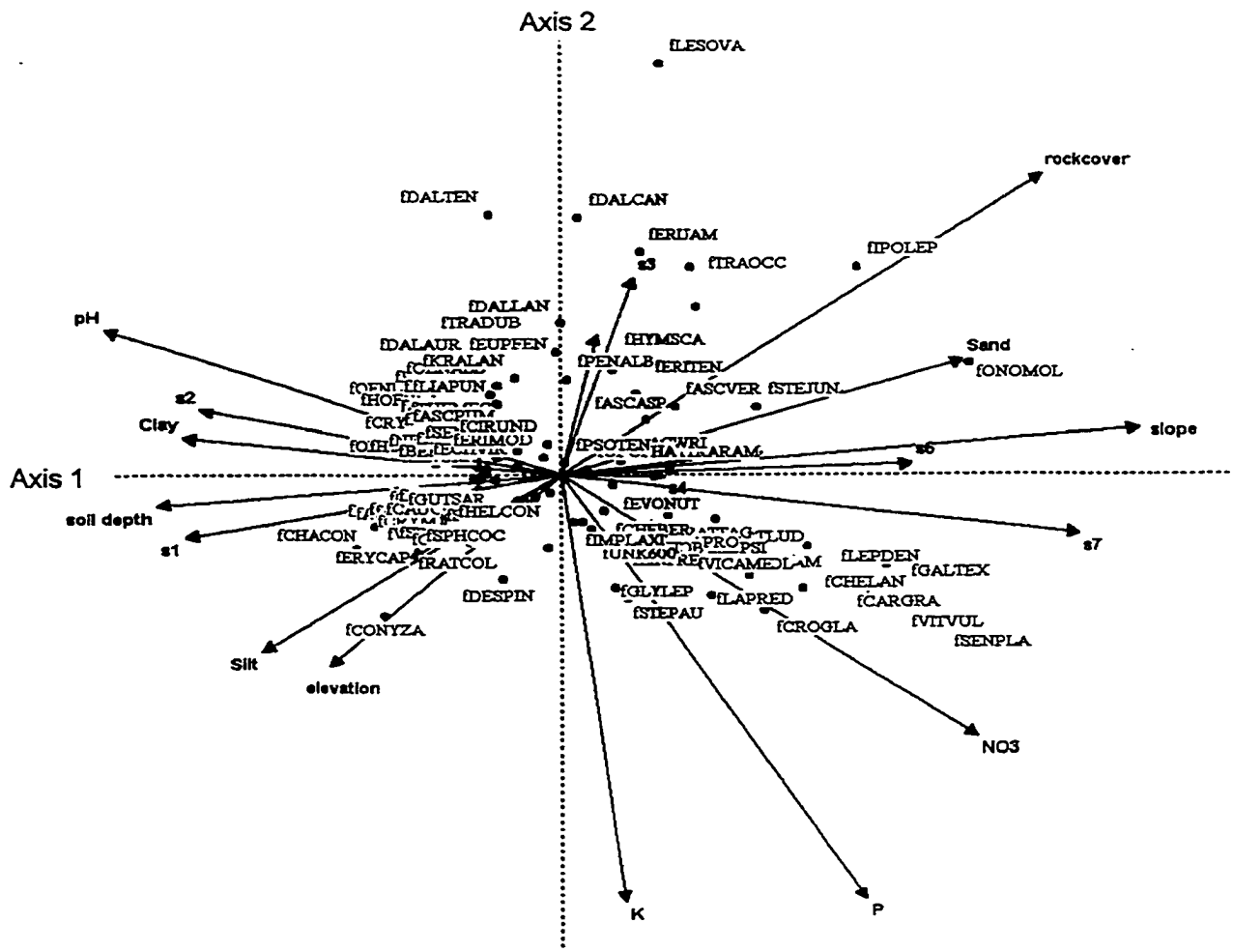
Legend Figure 8

CCA biplot of grass species related to the environmental variables. The codes represent the first three letters of the two word Latin name preceded by a "g" for grass species. Tall grass species are most correlated with the nitrogen gradient, as well as increased rock sizes and slope. Some of the species include: Agropyron smithii, Bouteloua ericoides, Bromus tectorum, Chloris verticillata, Digitaria cognata, Elymus canadensis, Eragrosits spetabilis, Panicum obtusum, Panicum virgatum, Poa fenleriana, Setaria leuchopila, Sorghastrum nutans, Tridens muticas. Shorter grass species are located on the left side of the ordination diagram and influenced more by smaller rock sizes, increased soil depth, clay and silt. These species include: Arisitda oligantha, Aristida purpurea, Buchlow dactyloides, Bouteloua gracilis, Hilaria jamesii and Muhlenbergia torreyi.


Axis 2
Axis 1
rockcover
s3
gSCHSCO
gSIICOM
northness
pH
gBOUHIR
gLYCPHE
Sand
s2
Clay
slope
gARIPUR
gBOUCUR
gANDGER
s5
gSORNUT
s6
gBUCDAC
gVULOCI
gANDSAC
gPOAFEN
gELYCAN
gMUHTOR
gSIIHYS
gPANHAL
soil depth
gBOUGRA
gBROTEC
s7
s1
gANDBAR
gBOUERI
gARIOLI
gHILJAM
gPANVIR
gSPOCRY
gERASPE
eastness
gPANOBT
gAGRSMI
gCHLVER
gHORPUS
gTRIMUT
gSETLEU
Silt
gDIGCOG
elevation
NO3
K
P

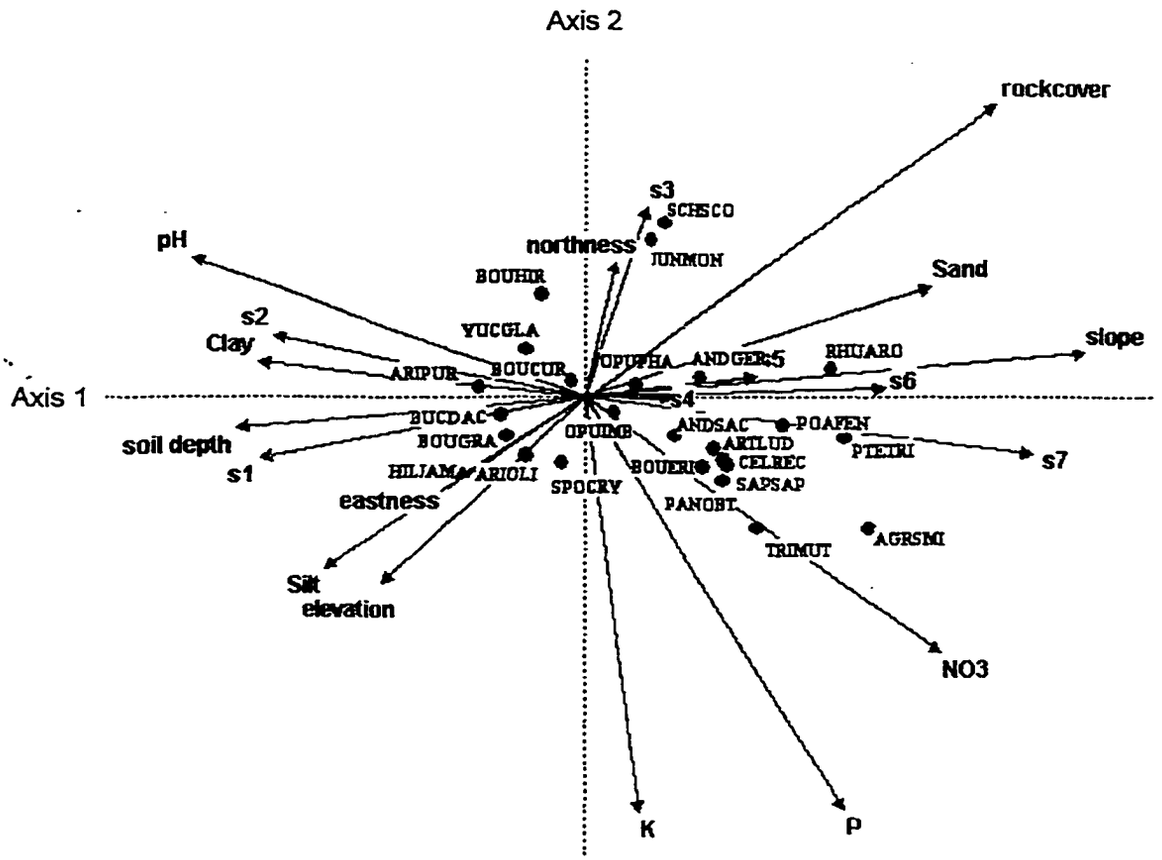
Legend Figure 9

CCA biplot of forb species related to the environmental variables. The codes represent the first three letters of the two word Latin name preceded by an "f" for forb species. The highest frequencies of forbs are clustered in the center of the ordination. Species located toward the fringes have increasing resource and habitat needs. For example, Lappula redowski, Carex gravida, Cheilanthes lanosa, Croton gladulosus, Galium texense, Lepidium densiflorum, Senecio plattensis, and Vitus vulpina are found in environments dominated by larger rocks, increased slope and high amounts of nitrogen and phoshorus. Onosmodium molle is found in sandy soils dominated by high slopes and large rocks. Dalea candidum, Dalea tenufolia, Erigrostis jamesii, Lesquerella ovalifolia, Ipomoea leptophylla, and Tradescantia occidentalis inhabit areas with increased rock cover and smaller rock sizes.


Axis 2
Axis 1
rockcover
pH
Sand
slope
soil depth
Silt
elevation
NO3
K
P
s1
s2
s3
s4
s6
s7
fLESOVA
fDALTEN
fDALCAN
fERIJAM
fTRAOCC
fIPOLEP
fDALLAN
fTRADUB
fDALAUR
fEUPFEN
fKRALAN
fHYMSCA
fPENALB
fERITEN
fONOMOL
fASCVER
fSTEJUN
fASCASP
fLIAPUN
fCIRUND
fERIMOD
fPSOTEN
fGUTSAR
fHELCON
fEVONUT
fCHACON
fSPHCOC
fERYCAP
fRATCOL
fDESPIN
fCONYZA
fIMPLAXI
fUNK600
fVICAMEDLAM
fLEPDEN
fGALTEX
fCHELAN
fCARGRA
fGLYLEP
fLAPRED
fSTEPAU
fCROGLA
fVITVUL
fSENPLA

Legend Figure 10

CCA species ordination biplot showing the location of the 25 greatest species abundances in relation to the environmental variables. The majority of the abundant species occur in areas with increased slope, larger rock sizes and more available nutrients. Bouteloua gracilis, the most abundant species at Black Mesa, is associated with other short grasses and gradients that represent grassland areas. Bouteloua curtipendula, the second most abundant species is found at the center of the ordination biplot, located in grassland and shrubland environments.


Axis 2
Axis 1
rockcover
s3
SCHSCO
northness
JUNMON
pH
Sand
BOUHIR
s2
Clay
YUCGLA
slope
OPUPHA
ANDGER5
RHUARO
ARIPUR
BOUCUR
s6
s4
BUCDAC
ANDSAC
POAFEN
soil depth
BOUGRA
OPUIMB
ARTLUD
PTEIRI
s7
s1
HILJAM
ARIOLI
BOUERI
CELREC
SPOCRY
SAPSAP
eastness
PANOBT
AGRSMI
TRIMUT
Silt
elevation
NO3
K
P