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DISSERTATION

PATTERN AND PROCESS AT A DESERT GRASSLAND-SHRUBLAND ECOTONE

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2001

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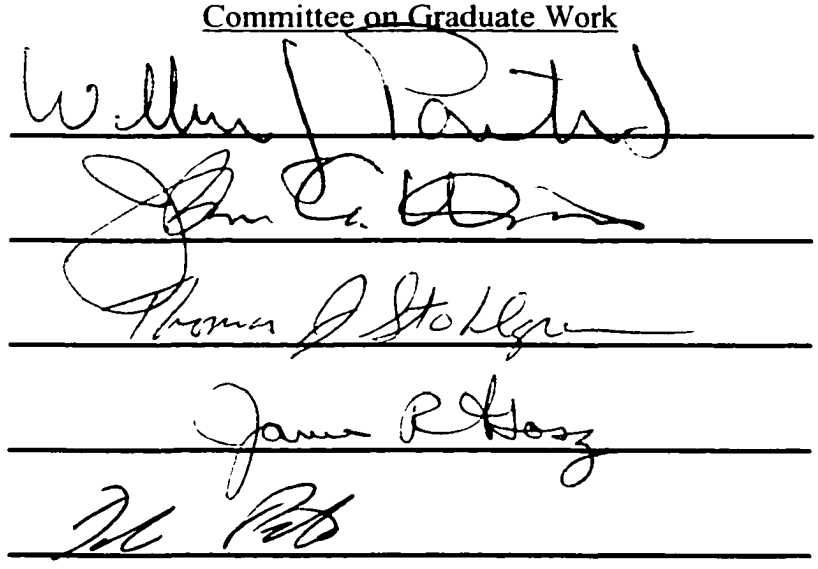
WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY TAMARA MARGRIT CAROLA HOCHSTRASSER ENTITLED PATTERN AND PROCESS AT A DESERT GRASSLAND-SHRUBLAND ECOTONE BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE DOCTOR OF PHILOSOPHY.

Committee on Graduate Work



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ABSTRACT OF DISSERTATION

PATTERN AND PROCESS AT A DESERT GRASSLAND - SHRUBLAND ECOTONE

Over the past century, shrub encroachment has occurred in desert grasslands all over the American Southwest. In the Northern Chihuahuan desert, most encroachment was due to creosotebush (*Larrea tridentata* [Sessé & Moc. ex DC.] Coville) expanding into black grama (*Bouteloua eriopoda* [Torr.] Torr.) dominated grasslands. Dominant plants contribute significantly to ecosystem structure and function, and grasses and shrubs differ fundamentally in their role in ecosystems. This dissertation investigated the influence of dominant plants, grasses and shrubs, on pattern and process at a desert grassland-shrubland ecotone. First, small-scale species coexistence patterns in microsites around dominant grasses (*B. eriopoda*) and shrubs (*L. tridentata*) were compared. Second, small-scale patterns were related to landscape scale species richness. Third, a gap-dynamics simulation model (ECOTONE) was used to investigate mechanisms that could create some of the patterns observed.

Contrary to expectations, subdominant species abundance was lower in microsites around grasses than in microsites around shrubs. Different functional groups of subdominant species had a different distribution in microsites. When extrapolating to the landscape, it was found that perennial species richness is related to the distribution of dominant plants across scales from the plant to the landscape, whereas annual species richness seems to be mainly influenced by disturbance. Both biotic and abiotic factors

contributed to the patterns observed across scales. Soil texture differences between microsites may explain differences in subdominant species abundance between the canopy area of plants and interspaces. In contrast, differences in subdominant species abundance between canopy areas of grasses and shrubs were most likely due to biotic factors, namely the morphological differences between the canopies of the dominant lifeforms. The use of the simulation model showed that black grama dominates the vegetation by a combination of intensive exploitation of water resources underneath its canopy and by its capacity to cope with soil disturbances, whereas creosotebush dominates by its long lifespan and low yearly biomass turnover rate. Replacement of black grama by creosotebush under the current disturbance and climatic regime would take a very long time. Similar to field observations, subdominant species abundance was higher in simulated creosotebush dominated landscapes than black grama dominated ones. It was concluded that the shift in the dominant lifeform by itself does not have a negative influence on plant species diversity at the ecotone investigated. On the contrary, the addition of shrubs to the vegetation increases spatial heterogeneity and has a positive effect on the overall diversity of the vegetation in an ecotone situation. Indirect processes induced by creosotebush that likely can be linked to species loss seem to only be important in areas where creosotebush dominates large extents of vegetation. Furthermore, other processes than shrub encroachment, such as human activities and drought, may contribute to species loss during desertification.

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TABLE OF CONTENTS

I. INTRODUCTION

Degradation of drylands (including arid, semi-arid and sub-humid regions), often called desertification, has been observed all over the world, and has been attributed to a combination of human activities and climatic factors (UNCED 1992). Overuse of natural resources and drought lead to soil erosion and loss of vegetation cover which is often combined with encroachment by woody plants (Schlesinger et al. 1990, Van Auken 2000). An important implication of this change for local economies is the loss of forage for livestock and a reduction of agricultural production (Darkoh 1998). The extended consequences of dryland degradation include famine, migration of populations, and disease (Darkoh 1998). To prevent such disasters in the future, large political and scientific efforts are underway to restore degraded lands and develop sustainable management strategies (UNCED 1992, de Soyza et al. 1998, Puigdefábregas 1998, Peters and Herrick 2001). Specifically, a scientific understanding of the variability of dryland systems in space and time, and of the fundamental processes that contribute to their resilience to climatic variability is helpful to the political leaders and communities responsible for dryland management (Thomas 1997).

Because the resilience of drylands may largely depend on their diversity, a major concern from an ecological point of view is the loss of species during dryland degradation (Huenneke and Nobel 1996). Human activities that contribute to this loss are grazing of domestic livestock, introduction of non-native plants and animals, creation of water sources, and wood harvesting. These activities induce ecological processes that

contribute to species loss, by changing the competitive environment of species and redistributing the resources for plant life (Huenneke and Nobel 1996). In particular, ecological processes may be fundamentally altered when the dominant lifeform shifts from grasses to shrubs during land degradation (Schlesinger et al. 1990). The abiotic changes that occur during shrub encroachment are relatively well understood, but how the biotic changes affect plant species diversity has not been investigated.

The objective of this dissertation was to investigate how a shift in the dominant lifeform, from grasses to shrubs, influences plant diversity. I hypothesized that a change in the dominant lifeform may contribute to a loss in species diversity, and investigated the possible mechanisms that could relate a loss in species diversity to a shift in dominant plants. Since I was interested in both structural and functional changes that occur during shrub encroachment, one of the aims of this research was to develop an integrated approach to the role of dominant plants in ecosystems. In particular, I combined expertise in the spatial analysis of vegetation pattern with insights from simulation modelling of ecosystems. These two subfields of ecology are often not well integrated, despite the strong relationship between ecological structure and function (Juhász-Nagy 1984, Turner 1989). Focusing on the dominant plants appears particularly promising for bridging the gap between these two subdisciplines, and has been used previously to address the relationship between pattern and process (Watt 1947, van der Maarel 1996).

The research for this dissertation was conducted at the Sevilleta Long-Term Ecological Research (LTER) site in central New Mexico (Gosz 1992, http://sevilleta.unm.edu). Over the past century, shrub encroachment of grasslands has been observed throughout the American Southwest (Van Auken 2000). In the Rio

Grande valley, where the research site was located, creosotebush (*Larrea tridentata* [Sessé & Moc. ex DC.] Coville) has expanded into black grama (*Bouteloua eriopoda* [Torr.] Torr.) dominated grasslands, known as desert grasslands (Gardner 1951, Grover and Musick 1990). The research was conducted at a desert grassland - shrubland transition zone or ecotone, located at the northern edge of creosotebush dominated areas in the Rio Grande valley. Three specific objectives were addressed in this dissertation. The first objective was to compare the influence of shrubs and grasses on small-scale species coexistence patterns. The second objective was to relate these small-scale species coexistence patterns to landscape scale species richness, since the landscape scale is important for management decisions. The third objective was to test what ecological mechanisms could create the patterns observed, using a simulation model.

Specific objective 1 (Chapter 2). To address my first specific objective, I compared species abundance and richness in microsites around dominant plants, both grasses and shrubs. The importance of distinguishing between microsites around plants has long been recognized by ecologists interested in ecosystem functioning, but this distinction has less often been used in spatial pattern analysis (Charley and West 1975, Shmida and Whittaker 1981). The method of analysis of the spatial pattern used for this study was specifically designed to gain insight into the average species composition and abundance in microsites around dominant plants, rather than to describe the small-scale species coexistence patterns in detail. This approach was selected because the goal of this study was to provide information about patterns that can be related to processes.

Specific objective 2 (Chapter 3). For my second specific objective, the importance of dominant plants for explaining species diversity patterns was compared to

other factors across scales, from the plant to the landscape scale. Apart from the dominant plants, the factors (or system properties) investigated were soil texture and disturbance. I developed methods to describe the variability of these factors, and related these measurements to species richness across scales. Insights from this study may help to extrapolate findings from small-scale studies to the landscape scale, where management decisions must be made.

Specific objective 3 (Chapter 4). I modified a gap-dynamics simulation model (ECOTONE, [Peters submitted]) to evaluate the influence of the dominant shrub (*L. tridentata*) and grass (*B. eriopoda*) species on subdominant functional group abundance and composition. Biological differences between the dominant grass (*B. eriopoda*) and the dominant shrub (*L. tridentata*) were evaluated, and a first attempt was made to incorporate feedback loops between these species and the abiotic environment into the model. Both the biotic characteristics of the dominants and abiotic changes induced by these species were expected to influence subdominant functional group abundance and composition.

The last chapter (Chapter 5) of this dissertation contains a summary of the findings from this research and conclusions.

Nomenclature throughout this dissertation follows: USDA, NRCS. 2001

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II. DIFFERENCES IN SUBDOMINANT SPECIES DIVERSITY AND SOIL TEXTURE IN MICROSITES AT A DESERT GRASSLAND-SHRUBLAND TRANSITION ZONE

Introduction

The role of subdominant plants in ecosystems has become increasingly recognized with the debate on the relationship between ecosystem functioning and biodiversity (Tilman et al. 1997, Walker et al. 1999). Subdominant species can complement dominants by performing different ecosystem functions, such as nitrogen fixation (Tilman et al. 1997). They also may play an important role in ecosystem resilience and stability if they are similar to dominant species in their contribution to ecosystem functioning, but different in their response to environmental change (Walker et al. 1999). Furthermore, invasive species may first be present as subdominants in ecosystems that they later come to dominate (Mack et al. 2000).

Subdominant species in vegetation often occur more abundantly in some microsites than in others (Shmida and Whittaker 1981, Beatty 1984, Gibson 1988). In many vegetation types, microsites are created by the presence of the dominant plants, and vegetation dynamics depend on the lifecycle of these plants (Watt 1947). Several studies have related small-scale species coexistence patterns to microsites around dominant plants (Muller 1953, Shmida and Whittaker 1981, Lightfoot 1991). These studies usually investigated coexistence patterns around shrubs and often only annual species were studied. However, different functional groups of subdominant species may occur more frequently in certain types of microsites than in others, and their spatial distribution may

depend on the lifeform of the dominant species (Olsvig-Whittaker et al. 1992, Belsky 1994).

A change in the dominant lifeform has been observed over the past century in desert grasslands where shrub encroachment occurred (Buffington and Herbel 1965, Grover and Musick 1990, Van Auken 2000). Most encroachment in the northern Chihuahuan desert has been by creosotebush (*Larrea tridentata* [Sessé & Moc. ex DC.] Coville) and mesquite (*Prosopis glandulosa* Torr.) expansion into black grama (*Bouteloua eriopoda* [Torr.] Torr.) dominated grasslands. This shrub encroachment typically leads to changes in the abiotic environment of these desert grasslands that persist through positive feedback loops (Schlesinger et al. 1990). The shift in the dominant lifeform during encroachment may also have important consequences in terms of the suitability of microsites for subdominant plants and changes in subdominant species composition may alter ecosystem stability over time. In this study, I wanted to determine how the structure created by two dominant lifeforms, shrubs and grasses, affects the distribution of subdominant species at a desert grassland-shrubland transition zone. Differences in subdominant species abundance in microsites around these two dominant lifeforms have not been directly compared and it is unclear how species diversity varies between microsites created by the structure of these lifeforms.

Microsites provide an appropriate scale for linking diversity patterns to mechanisms creating these patterns (Silvertown and Wilson 1994). Subdominant plants are sensitive to both competitive interactions with the dominant plants in the microsites and to variation in resources that may exist in these microsites. In this study, I distinguish three types of microsites around plants: (1) the canopy - influenced by the

aboveground structure of the plant; (2) the interspace - the space between aboveground structures of neighboring plants of the same species; and (3) the canopy edge - a transitional zone between the canopy and the interspace. Competitive interactions between subdominant and dominant species in these microsites are related to their root distribution, their phenology and their longevity (Schenk et al. 1999, Reynolds et al. 2000). The two dominant lifeforms compared in this study differ strongly concerning these characteristics. The shrubs (*L. tridentata*) have an extensive root system which is widespread around their canopy, whereas the grasses (*B. eriopoda*) have their roots concentrated beneath their canopy (Gile et al. 1998, Gibbens and Lenz in press). Water use of creosotebush (*L. tridentata*), an evergreen C3 species, is very opportunistic in time, whereas black grama (*B. eriopoda*), a C4 species, is only actively growing during the monsoon season between mid July and October (Kemp 1983, Reynolds 1986). *L. tridentata* is long-lived (ca. 400 years), whereas *B. eriopoda* was found to have a medium lifespan (ca. 40 years) (Nelson 1934, Miller and Huenneke 2000).

Resources in microsites around these dominants may also differ. Shrubs affect biogeochemical processes differently than grasses because of the shading effect of their canopy on the soil and/or because of differences in litter quality between the two lifeforms (Kieft et al. 1998, Gill and Burke 1999). Generally, both grasses and shrubs accumulate soil organic matter and nutrients underneath their canopy, but the spatial and temporal variability of soil nutrient concentrations is higher in shrublands than in grasslands (Kieft et al. 1998, Cross and Schlesinger 1999). Because soil texture influences water and nutrient availability, it can be used as an indicator for these differences among microsites (Kieft et al. 1998, Hook and Burke 2000). Therefore, the

competitive as well as the abiotic environment in these microsites varies, both between canopy areas of plants and interspaces as well as between lifeforms. Thus, I expected that these factors would affect subdominant species abundance differently in these microsites.

The objective of this study was to investigate how the occurrence of subdominant plants may be influenced by the structure of two dominant lifeforms and soil texture differences between microsites at a grassland-shrubland transition zone. Microsites can be compared in two different ways: either the canopy areas of plants and interspaces around individual plants are compared, or microsites around grasses and around shrubs. The first type of comparison was made for my first and second specific objective, whereas the second type of comparison was used to address my third specific objective.

The first specific objective was to compare total subdominant species abundance and richness in microsites underneath the canopy of plants and interspaces between plants. I expected higher abundance and richness of subdominant plants in shrub canopies than between shrubs in interspaces (Shmida and Whittaker 1981, Guo and Berry 1998). In contrast, around the dominant grass (*B. eriopoda*), I expected only small differences between microsites, both in terms of soil texture characteristics and subdominant species abundance, since soil characteristics in desert grasslands are more homogeneous compared to shrublands (Schlesinger et al. 1996). My second specific objective was to test if different species, functional groups, and life-stages of subdominant plants occupy different microsites within each lifeform. Finally, as my third specific objective, I wanted to compare the abundance, species richness and species overlap of microsites around grasses versus shrubs. I hypothesized that, because of the

desertification processes following shrub encroachment (Whitford et al. 2001), subdominant species abundance and richness in all microsites around shrubs (*L. tridentata*) would be lower than in microsites around grasses (*B. eriopoda*).

Methods

I. Site description.

The study was conducted at the Sevilleta Long-Term Ecological Research (LTER) site (http://sevilleta.unm.edu) situated in central New Mexico (latitude: 34°21'N; longitude: 106°53'W; 1650 m ASL). This site is located in the transition zone between Great Plains grassland, Great Basin shrubland and Chihuahuan desert (Gosz 1992). The average temperature (1916-1995) at a nearby weather station in Socorro, NM, ranges from 2.6°C in January to 24.6°C in July, mean precipitation is 232 (± 79 SD) mm (Hochstrasser et al. submitted). Domestic livestock has been excluded from this site since 1973 but native herbivores, such as jackrabbits and pronghorn antelope, are still lightly to moderately grazing the site.

II. Sampling.

I selected a *B. eriopoda* - *L. tridentata* dominated transition zone that was free of any obvious human disturbance, such as old roads or fence lines, and which exhibited a gradual transition from grassland into dense shrubland. A 100 m wide and 500 m long transect subdivided into 10 m x 10 m plots was located perpendicular to this transition zone for orientation. In each of the 10 m x 10 m, plots I visually estimated the area that was occupied by patches of shrubs and the intensity of disturbance. When less than a third of the plot had open ground or early successional vegetation on it, the intensity of disturbance was considered "low", and when more than a third of the plot exhibited these

characteristics it was considered "high". For sampling, I randomly selected 45 out of the 500 plots with the condition that at least 8 of them were in each of the following 4 classes: low disturbance and low dominance of *L. tridentata* (< 15%), low disturbance and high dominance of *L. tridentata* (≥ 15%), high disturbance and low dominance of *L. tridentata*, and high disturbance and high dominance of *L. tridentata*. I sampled the abundance of subdominant plants as well as surface soil in microsites around dominant shrubs (*L. tridentata*) and dominant grasses (*B. eriopoda*). Because plants can affect surface soil texture in arid environments (Cornet et al. 1992), I measured surface soil texture (0-7 cm) differences between microsites as an indicator of differences in abiotic conditions in these microsites. Sampling of microsites was conducted in September of 1997, at the seasonal peak of herbaceous growth.

Soil sampling. Any number of samples over 30 is generally considered sufficient to describe spatial variation of variables (Rossi et al. 1992). To save time, I sampled soil texture in 34 out of the forty-five 10 m x 10 m plots selected for sampling subdominant plants. I collected 119 soil samples from microsites around the dominant plants (shrub canopy, shrub edge, grass canopy) and from the interspace. Soil samples from a given type of microsite were only collected in a given plot if this type was available on the plot (i.e., if there were no shrubs on the plot then no samples from shrub canopy and canopy edge were collected). Soil was collected from 0-7 cm depth. Each sample was a composite of 3 samples from the same type of microsite, but different random locations within each 10 m x 10 m plot.

Vegetation sampling. In the forty-five 10 m x 10 m plots selected for sampling, microsites around a total of 167 individuals of the dominant grass (*B. eriopoda*) and 115

individuals of the dominant shrub (*L. tridentata*) were sampled. The number of shrubs and grasses sampled in each plot depended on the availability of plants of each dominant species. Between 0 and 5 individuals were randomly selected for sampling in each plot. The shrub canopy microsite was defined as the area underneath the canopy where it was multi-layered, shading the ground for most of the day. Often litter had accumulated in this microsite. I approximated this microsite with a circle, varying in radius according to the shape of the canopy (inverted-cone shape or hemispherical [de Soyza et al. 1997]). The radius was smaller in relation to the radius of the actual leaf canopy in inverted-cone shaped shrubs than in hemispherical shrubs, because sunlight and wind could penetrate further into the canopy underneath inverted-cone shaped shrubs (personal observation). The shrub canopy microsite was approximated with a circle that was on average 75 % of the radius of the leaf canopy of the shrub (Figure 2.1). Correspondingly, the canopy edge of shrubs was defined as a ring around the circular canopy area. Its width was twice the difference between the radius of the canopy area (as defined above) and the leaf canopy. Three circles with the same radius as the canopy area were sampled in the interspace immediately adjacent to the canopy edge area.

Due to the different shape of the grass canopy, microsites around this dominant species were defined differently. The canopy area was defined as the basal area of the grass. This area was usually elevated by a few centimeters in relation to the interspace. The canopy area included small openings in the canopy if the microtopography was not influenced by these openings. The area of the grass canopy was approximated with an elliptical shape and the shortest and longest diameters were measured. The canopy edge was defined as the transitional zone, between the microtopographic elevation of the

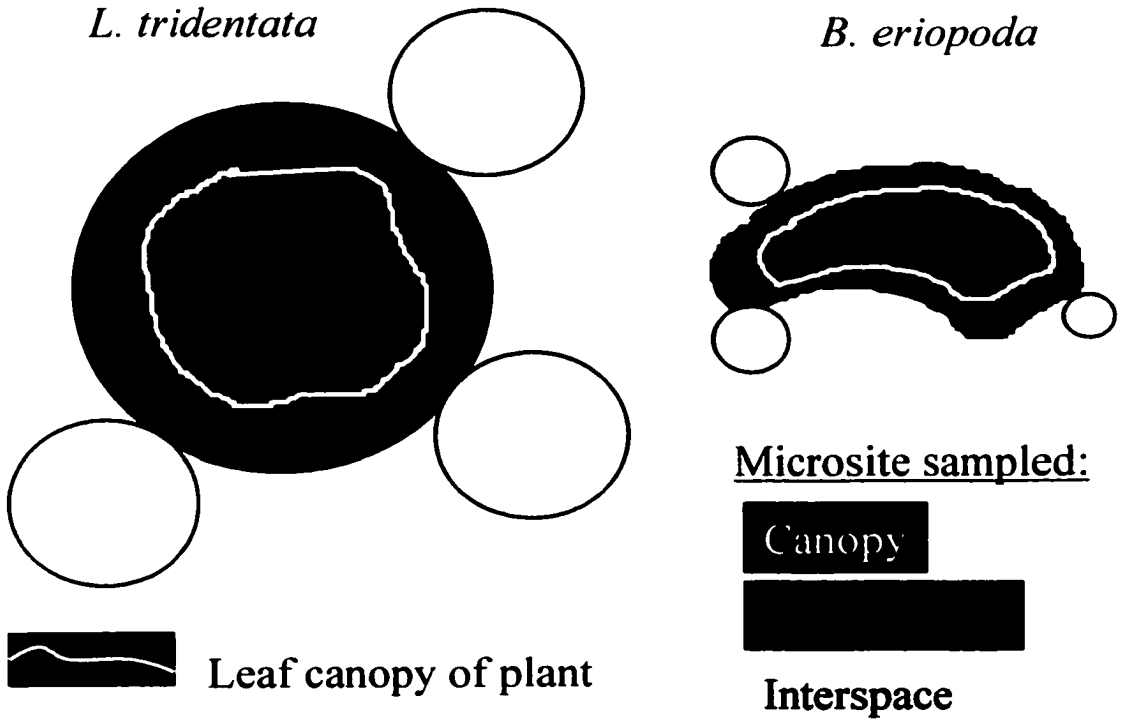

Figure 2.1. Sampling plots around individuals of the dominant shrub (*Larrea tridentata*) and the dominant grass (*Bouteloua eriopoda*), viewed from above.

canopy and the interspace. This microsite was still somewhat influenced by the canopy of the grass as single stems may extend into this area, but are not rooted there. Based on the average width of this transitional zone, I used a band of 3 cm width around the grasses as the standard measurement of this microsite. The radius of circular plots in the interspace between grasses was equal to the shorter of the two radii of the canopy ellipse, except in cases where the interspace between grasses was too small. In these cases I used a circular plot with the longest radius possible (Figure 2.1).

The total area of each microsite as defined above was sampled. Therefore, my sample plot size was variable according to the microsite and size of the plant. I selected this approach in order to include rare plants and seedlings that may have been missed using sample plots that did not maximize the area sampled within each microsite. Furthermore, this method was easily adapted to individual microsites of different sizes. In each sample plot, I identified all individual plants to the species level and determined their abundance (number of plants/microsite). Canopy cover (as a percent of the microsite) was estimated for grasses spreading in continuous clumps or rings that could not easily be separated into individuals. To compare species abundance between these grasses and other plants, this cover estimate was translated into a number of grass subunits that was calculated by determining how many subunits of a certain size could exist in the area covered. The size of a subunit varied with the cover of the grasses according to an empirical function (based on field observation), because subunits increase in size as cover increases:

$$S = 0.59*C^{0.21}$$

where S = size of the subunit and C = cover of the clonal species in the microsite (between 1 and 100). Once the size of the subunit was determined, I calculated the number of subunits in the microsite, by dividing the area occupied by the grass by S.

III. Analyses

Soil samples. Air-dried soil samples were analyzed for texture using a modified hydrometer method that is particularly appropriate for soils with high sand content. In a first sieving, the soil was separated into large particles (rocks, > 2 mm) and fine particles. In a second sieving, after shaking a 40 g sub-sample over night in hexametaphosphate, I separated the sand (53 μm - 2 mm) from the fine fractions of the soil by wet sieving the soil through a 53 μm sieve. The fine fractions were then suspended in water and the percentages of silt and clay were determined using a hydrometer reading at 2 hrs and correcting for the viscosity of the solution. Soil fractions were calculated with adjustment for the difference between the oven- and air-dried weight of the soil (method by D. Reuss after [Gee and Bauder 1986]). Differences among all microsites were determined for each soil fraction separately, using a one-way analysis of variance (General Linear Model Procedure, SAS Institute Inc. 1988). I used Fisher's least significant difference test to examine differences between means (alpha = 0.05).

Vegetation data. Even though the shrub density generally increased across the transition zone, the subdominant species abundance data from the microsites exhibited stationarity along the transect, and could therefore be considered (in a statistical sense) samples from the same population (Chapter 3). The variable plot size of the microsites did not allow the comparison of the abundance of subdominant plants in these microsites directly because species abundance was strongly dependent on the area sampled (Chapter

3). However, to provide an overview of the data collected, I extrapolated subdominant species abundance and species richness of all samples to 1 m^2, by dividing the number of subdominant plants or species found by the area of the microsite sampled. This method of extrapolation can introduce errors in the analysis since the density of plants is not uniform in space; thus no statistical test was performed on these data.

To address my first specific objective, comparing the subdominant species abundance between microsites around single plants, I used an approach found to be appropriate to compare microsites with different areas in previous studies (Aguiar and Sala 1997, Kröel-Dulay et al. 2000). This method compares the proportion of area sampled in each microsite with the proportion of subdominant plants found: $\frac{IND_{ijk}}{IND_{ij.}}$ is compared to $\frac{A_{ijk}}{A_{ij.}}$ where IND is the number of individuals found, A is the area of the microsites (m^2), i = 1 (grass), 2 (shrub) for the dominant species around which microsites were sampled, j = 1, 2, ..., $n_{1,2}$, where n_1 = 167 (*B. eriopoda*) and n_2 = 115 (*L. tridentata*) is the number of samples, k = 1 (canopy), 2 (canopy edge), 3 (interspace) for the microsite sampled. Thus, the number of individuals found for each species in a given microsite was translated into a percentage of the total number of individuals found in all three microsites around the same dominant grass or shrub. Similarly, the area sampled in a given microsite was expressed as the percentage of the total area sampled in all three microsites around an individual of the dominant species. Some of the microsite samples around individual plants were aggregated for this comparison. 'Interspace' was a composite of the 3 interspace plots sampled around each individual. In some occasions, a small group of shrubs was considered equivalent to one individual since shrubs in dense groups appeared to function as a unit. For these shrubs, 'canopy' and 'canopy edge'

samples are a composite of samples from three individuals in that group. I performed a Wilcoxon signed rank test to determine if the percentage of plants found in the microsite was higher, equal to or lower than expected based on the percentage of area sampled in the microsite (alpha = 0.05) (Univariate Procedure, SAS Institute Inc. 1988).

To address my second specific objective, to test if different species and functional groups have a different abundance in canopies versus interspaces, I classified subdominant plants into functional groups according to their lifeform (forbs, grasses, subshrubs and succulents), their longevity (annual, perennial) and their photosynthetic pathway (C3, C4 and CAM). I compared the abundance of these functional groups between microsites and I related this analysis to a comparison of individual species abundance in microsites. Functional groups and species were analyzed only if they were represented by at least three individuals around at least five dominant plants sampled. Seedlings were analyzed separately.

In order to contrast microsites around grasses and shrubs, I compared the abundance of subdominant plants among all six microsites (grass canopy, grass edge, grass interspace, shrub canopy, shrub edge, and shrub interspace). For this comparison, I calculated the percentage of subdominant plants and area relative to the totals from all microsites in the 10 m x 10 m plots:

$\frac{IND_{jk}}{IND_{j.}}$ is compared to $\frac{A_{jk}}{A_{j.}}$, where IND is the number of individuals found in combined samples from 10 m x 10 m plots, A is the combined area of the microsites, and j = 1, 2, ..., 45 plots sampled, k = 1, 2, .., 6 (one of six microsites). I performed a Wilcoxon signed rank test to determine if the proportion of plants found in the microsite was higher, equal to, or lower than expected based on the proportion of area sampled in

the microsite (alpha = 0.05) (Univariate Procedure, SAS Institute Inc. 1988). Species richness of microsites was compared in a similar way. I calculated the total number of species occurring in each microsite, and summed these numbers for microsites around an individual plant. This method allowed me to determine the proportional species richness of each microsite, unaffected by species overlap between microsites.

The overlap of species lists between microsites was determined using Jaccard's Index (J):

$$J = \frac{a}{a + b + c}$$

where *a* is the number of species common to both microsites and *b* and *c* are the numbers of species that occur in microsite 1 or 2 only, respectively (Podani 1994). This index varies between 0 and 1, and expresses the probability that a species will occur in one of the two microsites compared, given that it occurred in one of them. Species overlap around individual plants sampled was not determined, because of problems introduced by variable sample plot size.

Results

I. Soil differences between microsites.

Sand content of the surface (0-7 cm) soil in the four microsites sampled ranged from 60 - 85 %, silt content from 5-20 %, and clay content from 8 - 25 %. Therefore, the soil texture varied from a sandy loam to loamy sand. The large particle (> 2 mm) content of the soil samples varied from 1 - 33 % and consisted mostly (about 98 %) of pieces of calcium carbonate (caliche). For both grasses and shrubs, sand content was higher in plant canopy areas than in interspaces (Figure 2.2). The interspaces had higher percentages of fine particles (silt and clay) and large particles than the canopy areas.

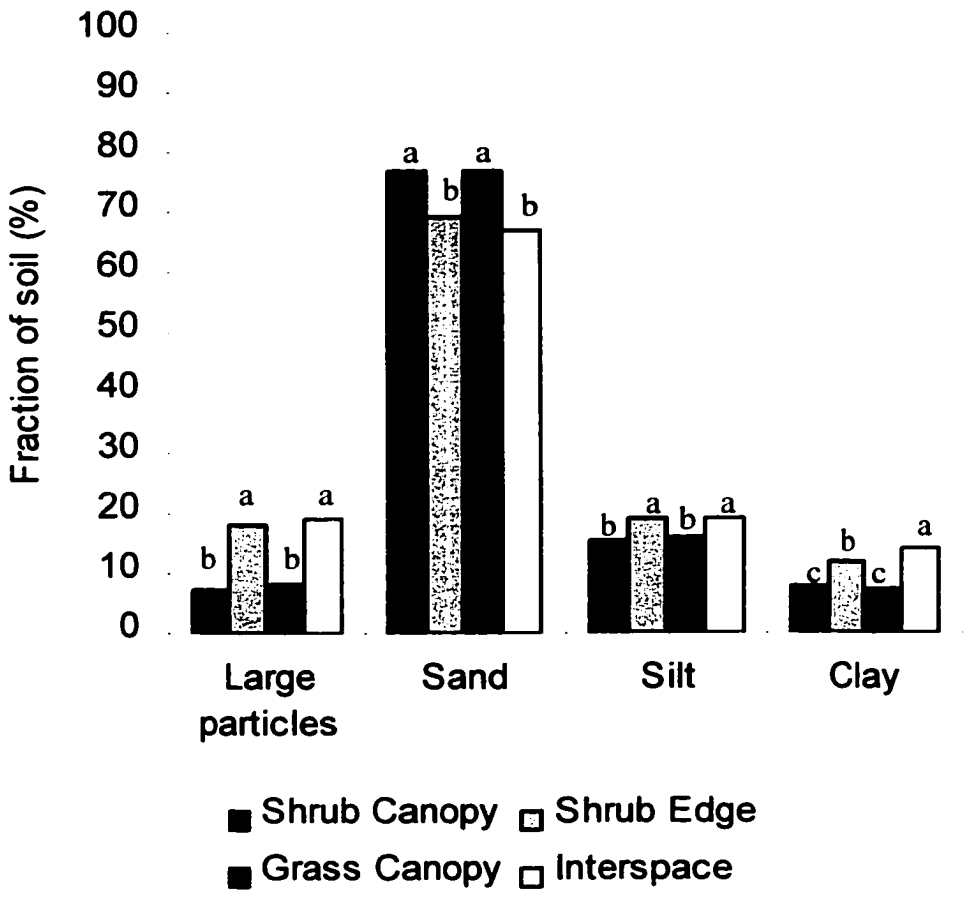

Figure 2.2. Soil texture of 0 - 7 cm depth in four microsites. Different letters indicate significantly different results (alpha = 0.05) within a texture class.

The soil texture of the shrub canopy edge was similar to the interspace, except for its lower clay content.

II. Overview of vegetation data

Microsites around shrubs (*L. tridentata*) were much larger than microsites around grasses (*B. eriopoda*) (Figure 2.3a). The canopy area sampled for shrubs was on average 0.79 m^2, whereas the canopy area of grasses was on average 0.14 m^2. Interspaces between shrubs were larger than the canopy area, whereas interspaces between grasses were similar in area to the canopy area. In the field, sample plots easily fit into interspaces between shrubs, whereas I sometimes had to reduce the size of sample plots to fit them into interspaces between grasses. Differences in area between the canopy edge of these lifeforms are a function of the definition of this microsite. For shrubs this microsite was defined as a much wider zone than for grasses, because of the different canopy structure of these lifeforms.

Species density was between 30 - 40 individuals/m^2 in microsites around shrubs (*L. tridentata*), whereas it was 20 - 30 individuals/m^2 around grasses (*B. eriopoda*) (Figure 2.3b). The density of subdominants was particularly low in the grass canopy, where only about 5 individuals/m^2 were found. Contrary to abundance patterns of subdominants, I found that species richness extrapolated to 1 m^2 was high around grasses (Figure 2.3c), particularly in the grass canopy edge, the smallest microsite. Linear extrapolation yielded between 15 - 20 species/m^2 around grasses and 5-15/m^2 species around shrubs. These differences in species abundance and richness between microsites may be partly due to differences in the area sampled (Figure 2.3a).

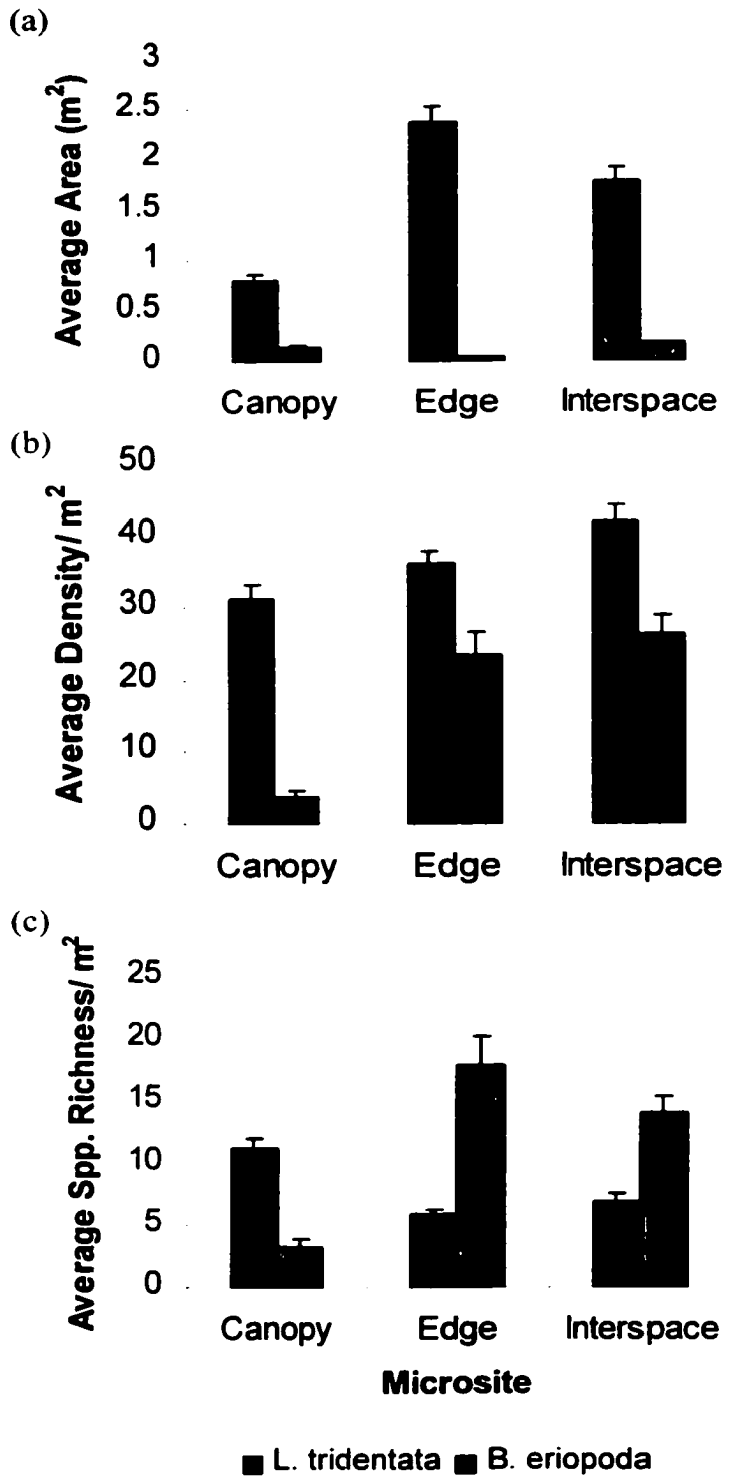

Figure 2.3. Characteristics of microsites around the dominant shrubs (*Larrea tridentata*) and the dominant grasses (*Bouteloua eriopoda*) (a) average area of sampling plots around individuals of the two dominant species (b) subdominant species abundance extrapolated to 1 m^2 (c) subdominant species richness extrapolated to 1 m^2. Error bars are standard errors.

A more detailed analysis using percentages rather than absolute numbers of subdominant plants follows below.

III. Total subdominant species abundance in microsites around individuals.

Microsites around individual plants were compared around grasses (*B. eriopoda*) and shrubs (*L. tridentata*) separately. The relative abundance of subdominant species in microsites around both lifeforms was found to be similar, so results will be discussed together (Figure 2.4). In both canopy areas, fewer subdominant plants were found than expected based their size. In the canopy edges, the abundance of subdominant plants corresponded to the area sampled, and the interspace samples contained more subdominant plants than expected.

IV. Differences in species and functional group abundance in microsites.

Different species and functional groups exhibited varying abundance in these microsites (Table 2.1). As mentioned in the methods section, only species and functional groups that were represented by at least 3 individuals around at least 5 dominant plants sampled were included in this analysis. Because of the different area sampled in each microsite, the number of functional groups or species included in this analysis is not a measure of species richness of these microsites. The objective of this analysis was to compare the abundance of individual functional groups or species between microsites (i.e. are plants more abundant in the canopy, canopy edge or interspace around the two dominants sampled?).

Around shrubs, annual C3 forbs, perennial C3 grasses and subshrubs were less frequent in the interspace than expected for the area sampled in this microsites (Table 2.1). The abundance of C3 perennial forbs corresponded to the area sampled in all

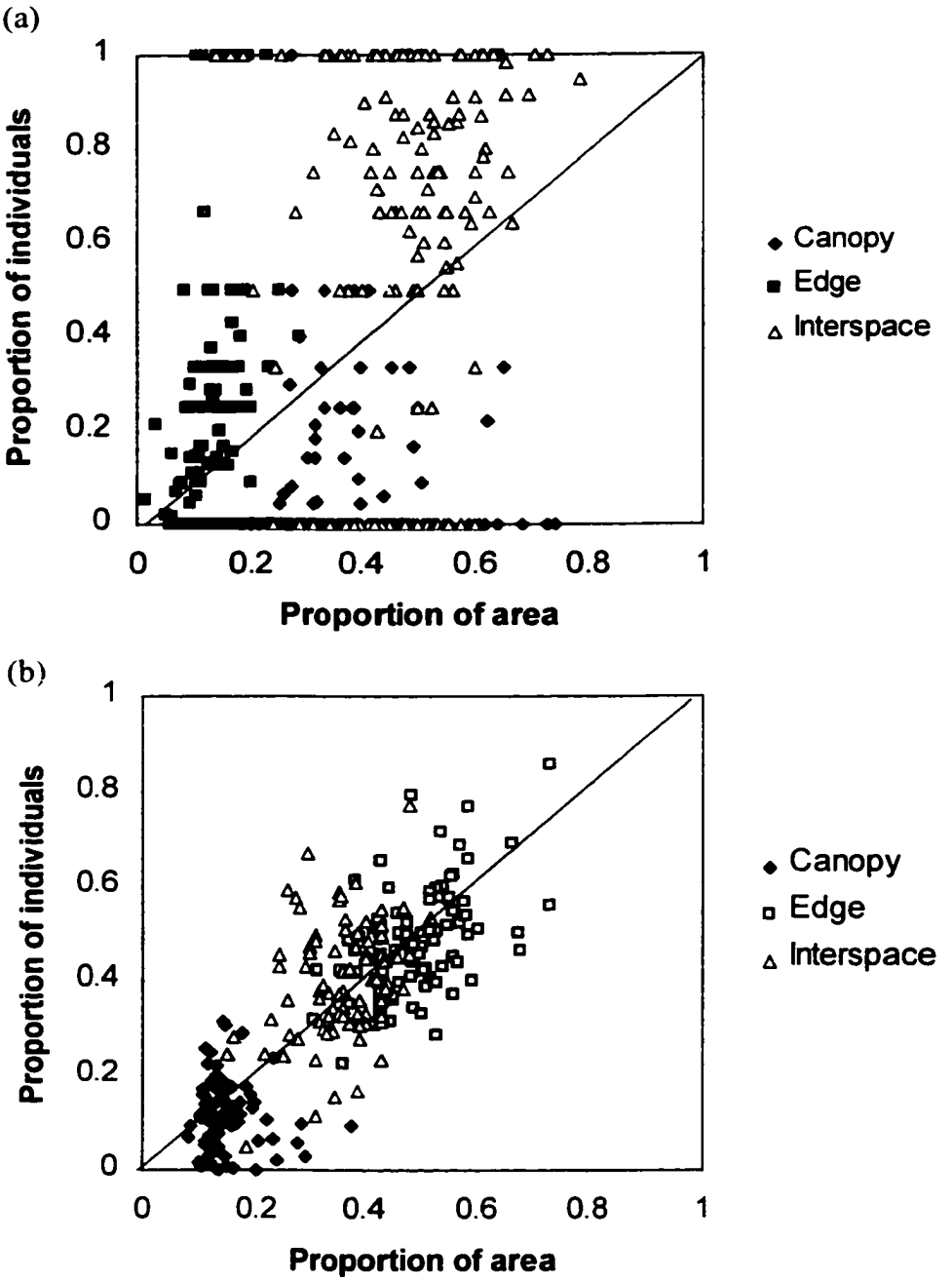

Figure 2.4. Proportion of area sampled in microsite versus proportion of subdominant plants found in each microsite at the individual plant level. (a) microsites around the dominant grass (*Bouteloua eriopoda*) (b) microsites around the dominant shrubs (*Larrea tridentata*).

microsites around shrubs. In microsites around grasses, C3 perennial forbs were more frequent than expected in the canopy edge and the interspace. The most abundant species composing this functional group in these microsites was *Caesalpinia drepanocarpa*. This species (and its functional group) was the only one that occurred more abundantly than expected in the canopy edge of the grasses. The abundance of C3 species, other than perennial forbs, was too low to be compared among microsites around grasses.

C4 species differed from C3 species in that they tended to occur more frequently in the interspace, both around grasses and shrubs (Table 2.1). This was particularly evident for C4 annual grasses and C4 annual forbs in grass interspaces. Microsites around shrubs did not show a clear pattern concerning the abundance of C4 annual forbs and C4 perennial grasses. Both of these functional groups occurred with similar abundance in all three microsites around shrubs. However, the species composing these functional groups occurred more frequently in specific microsites: the C4 annual forbs, *Chamaesyce* spp. tended to occur in the interspace, whereas *Salsola kali*, another C4 annual forb species, tended to occur in the shrub canopy. For C4 perennial grasses, I found that *Sporobolus* spp. tended to occur in the shrub canopy, whereas *Dasyochloa pulchella*, a short-lived perennial grass, tended to occur in the interspace. *B. eriopoda*, a subdominant in microsites around shrubs, tended to be less abundant in the shrub canopy than was expected based on area. C4 perennial forbs and succulents were not sufficiently abundant to compare frequencies between microsites.

The only seedlings that were sufficiently abundant to compare between microsites were those of *Sporobolus* spp., and the two dominants. Presence of seedlings indicates which microsite is most appropriate for germination; for the two dominant species it may

Table 2.1. Percentages of subdominant species and functional group abundance in the three microsites around individuals of the dominant species. The last row contains percentages of area sampled in each microsite for comparison. * indicates a significantly lower percentage of plants in relation to the percentage of area occupied by the microsite, # indicates a significantly higher percentage (Wilcoxon signed rank test, alpha = 0.05).

Microsite / Fct. group/ Species name	Shrub canopy	Shrub canopy edge	Shrub inter-space	Grass canopy	Grass canopy edge	Grass inter-space
C3 annual forbs	34	48	18 *			
C3 perennial forbs	18	48	34	12 *	30 #	59 #
Caesalpinia drepanocarpa (Gray) Fisher	16	47	37	12 *	32 #	56 #
Sphaeralcea wrightii Gray	13	60	28			
Sphaeralcea leptophylla (Gray) Rydb.	12	36	52			
Lesquerella fendleri (Gray) S. Wats	25	54	22			
C3 perennial grasses	92 #	8 *	0 *			
C3 perennial subshrubs and shrubs	33 #	51	16 *			
Gutierrezia sarothrae (Pursh) Britt. & Rusby	36 #	54	11 *			
C4 annual forbs	12 *	47	41	8 *	10 *	82 #
Chamaesyce serrula (Engelm.) Wott. & Standl.	2 *	46	52 #			
Chamaesyce serpyllifolia (Pers.) Small	3 *	47	51 #			
Chameasyce revoluta (Engelm.) Small	7 *	42	52			
Salsola kali L.	37 #	47	16 *			
Tidestromia lanuginosa (Nutt.) Standl.	3 *	50	48			
% Area	15	50	36	38	14	48

Table 2.1 - continued.

Microsite / Fct. group/ Species name	Shrub canopy	Shrub canopy edge	Shrub inter-space	Grass canopy	Grass canopy edge	Grass inter-space
C4 annual grasses	3 *	43 *	55 #	0 *	0 *	100 #
Bouteloua barbata Lag.	4 *	38 *	58 #	0 *	0 *	100 #
Monroa squarrosa (Nutt.) Torr.	3 *	52	45			
C4 perennial grasses	12 *	50	37	8 *	15 *	77 #
Aristida purpurea Nutt.	22	42	36			
Bouteloua eriopoda (Torr.) Torr.	13 *	47	41			
Enneapogon desvauxii Desv. ex Beauv.	7 *	53	40			
Dasyochloa pulchella (Kunth) Willd. ex Rydb.	10 *	47	43 #	4 *	4 *	92 #
Muhlenbergia torreyi (Kunth) A.S. Hitchc. ex Bush	19	49	32	0.4 *	15	85 #
Scleropogon brevifolius Phil.	13	45	42	0 *	9	91 #
Sporobolus contractus A. S. Hitchc.	52 #	34 *	14 *			
Sporobolus flexuosus (Thurb. ex. Vasey) Rydb.	25	64	11 *			
Seedlings of perennials						
Bouteloua eriopoda seedlings	4 *	41	55 #	0 *	0 *	100 #
Larrea tridentata seedlings	26	49	26 *	11	56	33
Sporobolus seedlings	31 #	50	19 *	5 *	23	72 #
% Area	15	50	36	38	14	48

also indicate the ability to replace one another. I found that seedlings of the grasses (*B. eriopoda*) occurred both around *B. eriopoda* plants as well as around shrubs, predominantly in the interspaces (Table 2.1). In contrast, seedlings of *L. tridentata* were most abundant in the canopy area of the shrubs, and significantly less abundant than expected (based on area) in all microsites around grasses as well as in the interspaces. Seedlings of *Sporobolus* species tended to occur in the canopy area of *L. tridentata*; whereas around *B. eriopoda* they occurred more frequently in the interspaces. This pattern corresponds to the distribution of adult *Sporobolus* plants which showed a tendency to occur in the shrub canopy.

V. Differences between microsites around grasses and shrubs

As shown in the previous analyses, relative subdominant species abundance was similar between microsites around grasses and shrubs. Furthermore, there were some similarities in functional group abundance between microsites around grasses and shrubs. In order to compare microsites around grasses and shrubs directly, I calculated percentages of subdominant abundance and species richness in each microsite at the plot level (see Methods). Results using this analysis correspond to the overall impression from the extrapolated data (Figure 2.3). Even in this analysis, different trends in subdominant species richness and abundance could be observed (Table 2.2). The percentage of subdominant plants was higher around shrubs than was expected for the percentage of area sampled. On average, microsites around grasses accounted for 14 % of the area sampled in a plot, but only 6 % of the subdominant plants occurred in these microsites. In contrast, compared to the area, species richness was higher in the grass canopy edge, grass interspace, and the shrub canopy.

Table 2.2. Percentages of subdominant species abundance and richness and seedlings of the dominants in the six microsites on the plot level. The last row contains the percentage of area sampled in each microsite for comparison. * indicates a significantly lower percentage of plants in relation to the percentage of area occupied by the microsite, # indicates a significantly higher percentage (Wilcoxon signed rank test, alpha = 0.05).

Microsite / Sub-dominant	Shrub canopy	Shrub canopy edge	Shrub inter-space	Grass canopy	Grass canopy edge	Grass inter-space
Abun-dance	11	46 #	36 #	0.3 *	0.9 *	5 *
Species richness	21 #	34 *	27 *	2 *	4 #	12 #
% Area	13	42	31	5	2	7

Table 2.3. Species overlap between species lists of microsites as measured by Jaccard's index.

	Shrub canopy	Shrub canopy edge	Shrub inter-space	Grass canopy	Grass canopy edge	Grass inter-space
Shrub canopy	1.00	0.74	0.70	0.30	0.45	0.57
Shrub canopy edge		1.00	0.80	0.27	0.39	0.60
Shrub interspace			1.00	0.29	0.46	0.71
Grass canopy				1.00	0.54	0.41
Grass canopy edge					1.00	0.58
Grass interspace						1.00

Species overlap among grass microsites was lower than species overlap among shrub microsites (Table 2.3). The lowest species overlap was found when the grass canopy area was compared to all shrub microsites. In contrast, the grass interspace had a relatively high overlap with shrub microsites, particularly the shrub interspace (Jaccard's index = 0.71). Therefore, the canopy areas of *L. tridentata* and *B. eriopoda* were more dissimilar than their interspaces in terms of overall species composition.

Discussion

Two types of comparisons between microsites were made in this study: a comparison between the canopy areas of plants and interspaces around individual plants, and a comparison between microsites around grasses and shrubs. The former comparison allowed me to examine differences in the structure of the vegetation created by single plants and the latter to illustrate changes in species composition that may occur during or after shrub encroachment into grasslands. I will first discuss the differences between microsites around individual plants and then differences between shrubs and grasses.

I. Differences between microsites around individuals.

Microsites around individual plants differed both in terms of their soil texture and in the abundance of subdominant plants and their species composition. The greatest contrast was found between plant canopies and interspaces. Most variables had intermediate values in the canopy edge microsite. Therefore, these microsites differed both in their environmental conditions and in the reaction of plants to these conditions.

Differences in environmental conditions between microsites. The similarity in soil texture between the grass and shrub canopy may be due, in part, to the sampling method. Soil samples under shrub canopies were collected in a subdominant plant

canopy area. However, coarse particles have been found to accumulate underneath both grasses and shrubs in previous studies (Charley and West 1975, Kieft et al. 1998). The accumulation of coarse soil particles in the canopy area of plants is a result of differences in wind erosion between plants and interspaces. Large particles, or rocks, are less susceptible to erosion and therefore tend to be concentrated in interspaces. Soil texture can be related to nutrient and water availability in these microsites (Kieft et al. 1998, Hook and Burke 2000).

Apart from soil texture, these microsites may differ in other environmental conditions, including the competitive environment and their average temperature (Holmgren et al. 1997, Breshears et al. 1998, Kieft et al. 1998). It is unclear how the competitive environment in these microsites varies from the canopy areas of these species to the interspaces. This is because the roots of both dominant lifeforms extend into the interspaces and use interspace resources (Fowler 1986, Gile et al. 1998, Yonder and Nowak 1999). More studies are needed to determine if competition for resources differs among these microsites.

Differences in the response of subdominant plants to environmental conditions in microsites. Species belonging to the same functional group tended to occur in similar microsites. Adaptations of plants to the different environmental conditions in these microsites have been observed in similar environments (Belsky 1994). For example, amongst functional groups, C3 species occurred most consistently in the shrub canopy. This trend may be related to lower temperatures in this microsite (Breshears et al. 1998). C3 species have a lower temperature optimum for growth than C4 species (Kemp and Williams 1980). However, higher nitrogen levels in shrub canopies could also contribute

to this pattern. It was found that C3 species have a lower nitrogen use efficiency than C4 species (Brown 1978). Furthermore, C3 annuals increased with nitrogen amendments, whereas C4 annuals did not respond to these amendments in desert shrublands (Gutierrez and Whitford 1987).

Consistent with this pattern, C4 annuals were very abundant in the interspace between plants. Another study in the Chihuahuan desert found that C4 annuals (i.e. most summer annuals) were more abundant in the interspaces, whereas C3 annuals (i.e. most spring annuals) were more abundant in canopy areas of shrubs (Lightfoot 1991). Therefore, the abundance of annuals may vary seasonally among microsites. Studies of the Mojave desert suggest that this pattern may also vary geographically since annuals there are generally more abundant in shrub canopies (Muller 1953, Shmida and Whittaker 1981). However, Mojave desert annuals are mostly spring annuals (Ludwig et al. 1988) and their preferential occurrence in shrub canopies would therefore be consistent with the pattern observed in the Chihuahuan desert. My expectation that the shrub canopy would have higher subdominant species abundance than the interspace was based on previous studies in the Mojave desert (Muller 1953, Shmida and Whittaker 1981). Therefore, the differences in the abundance of spring and summer annuals between microsites may explain why, contrary to this expectation, my study found that the shrub canopy had a lower rather than a higher subdominant species abundance than the interspace. Further studies are needed to test the generality of the differences in annual species occurrence between microsites.

The phenology of species also is important for explaining species coexistence patterns (Reynolds et al. 2000). In a removal study, it was found that competition from

black grama (*B. eriopoda*) was affecting mainly summer annuals and spring annuals germinating in early winter (Baggs 1997). Perennials were less affected by competition from this dominant grass. I found that some (especially C3) perennial species could survive in the canopy edge of black grama. This may be explained by the highly seasonal activity of black grama; subdominant species using resources in spring, when black grama is not active, can survive in its neighborhood (Baggs 1997).

However, in some cases, species belonging to the same functional group did not exhibit similar distribution patterns. This may be partially due to the differences in seed availability that exist between microsites (Aguiar and Sala 1997, Bisigato and Bertiller 1999). These studies found that the seedling abundance is limited by seed availability in different microsites. Evidence from my study may be interpreted as supporting this observation. The high abundance of *Salsola kali* in shrub canopies as well as the occurrence of seedlings of both creosotebush (*L. tridentata*) and dropseed (*Sporobolus* species) close to adult plants may indicate that seed availability was important in determining subdominant species abundance in these microsites. *Salsola kali* is a tumbleweed and dead plants tend to get caught in the canopy of the shrubs (personal observation). However, contrary to (Aguiar and Sala 1997), very few subdominants occurred in grass clumps at my site, despite the high seed availability in this microsite (Hochstrasser, unpublished data).

The differences between subdominant species abundance found in these microsites indicates differences in their ecological requirements for environmental conditions. This supports the idea that these species are contributing to ecological resilience of these ecosystems (Walker et al. 1999). The spatial heterogeneity of

vegetation is an important characteristic: over time certain microsites within the vegetation may serve as refugia for the species composing the vegetation when large scale changes in climate occur (Beatty 1984). However, the suitability of these microsites for different species may also change over time (Fowler 1988, Primack and ShiLi 1991). Therefore, the results from this study have to be interpreted with caution.

II. Differences between grasses and shrubs.

The series of microsites described in this study differed greatly in their areas. Microsites around shrubs were larger than microsites around grasses. It has been found that area is an important factor in determining the suitability of these microsites for subdominant plants (McConnaughay and Bazzaz 1987, Hook et al. 1994). This may be a contributor to the observation that, contrary to an expected decrease in species diversity accompanying shrub encroachment, shrubs had a higher subdominant species abundance in the microsites around them than did grasses. Alternatively, this finding may be related to past disturbances, as shrub encroachment has been found to be linked to small scale disturbances and grazing (Grover and Musick 1990, Chew and Whitford 1992). Therefore, high subdominant species abundance around shrubs may be a legacy of past disturbances, especially in relatively recently invaded grasslands. It may be that after an initial increase in subdominant species abundance, slow processes of soil erosion and competition lead to subdominant species loss. However, this was not observed in my study.

Various sizes of microsites sampled around shrubs and grasses may also help explain why subdominant species abundance patterns differed from subdominant species richness patterns. In small areas with low subdominant species abundance - as in

microsites around grasses - species richness was found to be high. This corresponds to observations that the species-area curve is steepest at small scales (Weiher 1999). The area sampled in microsites around shrubs was larger, the abundance of subdominant plants was higher, and the number of species in relation to the number of plants was lower than in microsites around grasses. However, the size of the area sampled can not fully explain the relationship between species richness and abundance in these microsites and ecological differences among microsites may also contribute to these differences.

In general, differences in subdominant species abundance between microsites around shrubs were less pronounced than differences between microsites around grasses, and shrub microsites had a higher species overlap. This is contrary to the expectation that subdominant species abundance may be similar in grass microsites because of the relative homogeneity of soil resources (Schlesinger et al. 1996). However, the strong contrast between plant canopies and interspaces with respect to the presence of aboveground biomass counterbalances the relative homogeneity of soil resources in microsites around grasses. In comparison, shrubs have canopies which do not occupy the same physical space as subdominant plants, but simply add another layer to the vegetation structure (Belsky 1994). As a consequence, subdominant species abundance underneath shrub canopies is only slightly different from surrounding areas, whereas the canopy of the grasses can physically exclude subdominant species. Because this physical exclusion of subdominants does not occur under the shrub canopy, it seems that the heterogeneity added to the vegetation by shrub canopies during shrub encroachment has - at least initially - a positive effect on subdominant species diversity.

Conclusion

The small-scale heterogeneity of vegetation created by the presence of dominant plants influences, in a variety of ways, subdominant species abundance and composition, even in the case of the smallest microsite, the grass canopy edge. This indicates that the structural variability around dominant plants is important in contributing to the overall diversity of the vegetation. These findings correspond to many other studies pointing to the importance of dominant plant structure for subdominant occurrence patterns.

Subdominant species differ in their abundance in microsites around both dominant species, *L. tridentata* and *B. eriopoda*. Numerous differences in microenvironmental factors in these microsites may contribute to the patterns observed. One of these differences is soil texture. Variation in soil particle size may contribute to different subdominant abundance in canopy areas and interspaces. However, in times of shrub encroachment, canopy structure of the dominant species may come to play a more important role in influencing canopy area subdominant abundance.

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III. LANDSCAPE HETEROGENEITY AND SPECIES RICHNESS PATTERNS ACROSS SCALES AT A DESERT GRASSLAND - SHRUBLAND ECOTONE.

Introduction

Understanding species richness patterns at the landscape scale is important, as this is the scale most relevant to management decisions (Hobbs and Norton 1996, Gustafson 1998). However, the scale of species interactions, where the primary processes shaping species coexistence patterns occur, is the scale of individual plants (Huston 1999). Across scales, from the plant to the landscape, spatial heterogeneity is related to plant species richness and changes in species composition (Romme 1982, Juhász-Nagy 1992, Tilman and Pacala 1993). Therefore, understanding the spatial heterogeneity of the landscape may contribute to understanding species richness patterns at the landscape scale.

An operational definition of spatial heterogeneity includes two components: the system property of interest and its complexity or variability at a given scale (Li and Reynolds 1995). Multiple system properties are related to species composition and richness at different scales (Wiens 1989). In order to understand the relationship between spatial heterogeneity and vegetation composition, the complex pattern created by multiple factors has to be decomposed into patterns related to specific system properties that can be investigated separately (Urban et al. 1987). System properties of interest can include soil properties, topography, distribution of dominant plant species and disturbances (Collins and Barber 1985, Gibson and Hulbert 1987, Wierenga et al. 1987).

To understand the role of different system properties in creating and maintaining species diversity, multiple system properties were investigated in this study.

Variability (or heterogeneity) of system properties can be described by their patchiness across scales (Urban et al. 1987), or by their trend and/or variability at the scale of interest (Harner and Harper 1976, Li and Reynolds 1995). At any given scale, variability of the system property of interest is expected to peak as boundaries or ecotones are crossed (Neilson 1993). The existence of a boundary or ecotone in a given system property implies a certain homogeneity with regard to the property of interest within adjacent ecological systems, yet a distinctiveness between them. Many system properties exhibit boundaries at multiple scales (Krummel et al. 1987, Gosz 1993). Therefore, studies across multiple scales are needed to adequately describe the variability of ecological system properties. Multi-scale studies can also reveal how the strength of the relationship between the variability of system properties and species richness changes across scales (Urban et al. 1987, Rescia et al. 1997).

Variability in system properties can be related to species diversity because characteristics of species that help them to tolerate certain conditions may be linked to difficulties with tolerating others (Tilman and Pacala 1993). For example, trade-offs may exist between the ability of plant species to minimize their resource requirements and their tolerance of physical stress (Tilman and Pacala 1993, Holmgren et al. 1997). Another example of a trade-off is that high colonization ability and growth rate often seem to be linked to low competitive abilities of plants (Grime 1974, Huston and Smith 1987, Tilman 1994). Therefore, system properties that are indicative of environmental

conditions and disturbance may best be studied to understand changes in species composition and diversity across scales.

In arid environments, patches created by the presence of dominant plants can be associated with heterogeneity in environmental conditions across multiple scales (Cornet et al. 1988, Kieft et al. 1998, Ludwig et al. 2000). Variation in environmental conditions may determine where certain dominant species occur; alternatively the dominant plants can also modify the environmental conditions around them (Hallmark and Allen 1975, Wilson and Agnew 1992). The size of the patches dominated by a certain lifeform influences the characteristics of the environment in these patches (Ludwig et al. 2000). Heterogeneity created by disturbance at multiple scales is also common in arid environments (Boeken and Shachak 1994, McPherson 1995, Whitford and Kay 1999). During the last century, desert grasslands throughout the Southwestern United States have been grazed intensively by domestic livestock, which created a mosaic of patches exposed to different grazing intensities (Fredrickson et al. 1998, Nash et al. 1999). Mounds of kangaroo rats (*Dipodomys spectabilis*) also contribute significantly to the spatial heterogeneity of these grasslands by creating patches subjected to removal of biomass and soil turnover (Moorhead et al. 1988, Guo 1996). Therefore, heterogeneity in desert grasslands can be decomposed into variability in environmental conditions - as expressed by the variability of dominant plants - and variability due to disturbance. These two system properties can be used to study the relationship between spatial heterogeneity and species diversity.

Responses of organisms to system properties may vary between species and across scales (Wiens 1989). This may be the reason that systems properties have been

found to influence plant species or functional groups of species differently (Gibson and Hulbert 1987, Brosofske et al. 1999). In arid ecosystems, distributions of perennial and annual plant species diverge in relation to environmental conditions at regional scales (Danin and Orsham 1990, Kutiel et al. 2000, Hochstrasser et al. submitted). Therefore, these functional groups may have a different response to variability in system properties at the plant to the landscape scale, too.

The objective of this study was to determine the strength of the relationship between the variability in multiple system properties and species richness at a desert grassland-shrubland transition zone across scales. My specific objectives were to (1) describe the variability of these system properties at multiple scales; (2) relate it to species richness of perennial and annual species at each scale; and (3) investigate how variability in system properties and species richness are interrelated across scales. To address these objectives, I defined three scales: the landscape scale, the plant scale, and a scale intermediate between these two scales, the plot scale which is a scale of multiple plant neighborhoods (Figure 3.1). The landscape scale corresponded to the scale of a transition zone between grassland and shrubland (a 500 m long transect), the intermediate scale to 10 m x 10 m plots within the transect, and the plant scale to the scale of both dominant grasses (*Bouteloua eriopoda* [Torr.] Torr.) and shrubs (*Larrea tridentata* [Sessé & Moc. ex DC.] Coville). The variability of the distribution of dominant plants was investigated at all three scales. This was compared to the variability in soil texture at the scale of the transition zone and the variability in the intensity of disturbance at the plot scale.

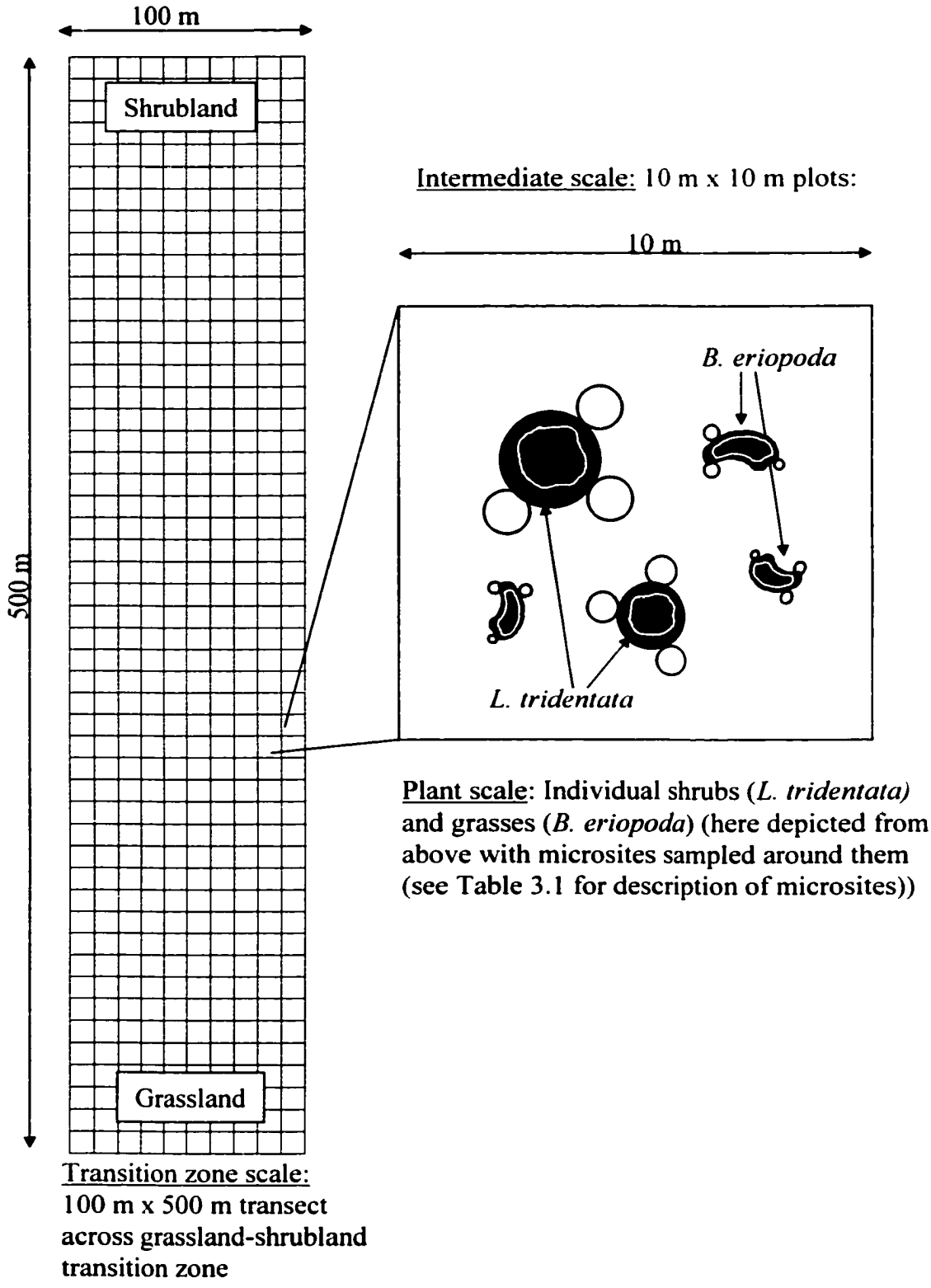

Figure 3.1. Definition of scales and sampling setup at each scale.

Methods

I. Site description

This study was conducted at the Sevilleta Long-Term Ecological Research site (http://sevilleta.unm.edu) in central New Mexico (latitude: 34°21'N; longitude: 106°53'W). This site is located within the transition zone among Great Plains grassland, Great Basin shrubland and Chihuahuan desert biomes (Gosz 1992). The average long-term (80 years) temperature at a nearby weather station in Socorro, NM (latitude: 34°03'N; longitude: 106°54'W), ranges from 2.6°C in January to 24.6°C in July; mean (± SD) precipitation is 232 (± 79) mm (Hochstrasser et al. submitted). Kangaroo rats (*Dipodomys spectabilis*) contribute significantly to small-scale disturbance at this site (Fields et al. 1999). Vegetation at this site is recovering from grazing by domestic livestock since 1973 (Ryerson and Parmenter in press). Grazing by native herbivores, such as pronghorn antelope and jackrabbits, occurs at light to moderate intensities.

II. Sampling

I selected a *Bouteloua eriopoda* (black grama) - *Larrea tridentata* (creosotebush) dominated transition zone that was free of any obvious human disturbance, such as old roads or fence lines, and exhibited a gradual transition from grassland into dense shrubland. This transition zone represented the northern edge of *L. tridentata* encroachment into *B. eriopoda* dominated grasslands. I used a 100 m wide by 500 m long transect, subdivided into a grid of 10 m x 10 m plots, located perpendicular to the transition zone. The 10 m x 10 m plots were assumed to be sufficiently large to encompass heterogeneity observed at the intermediate scale, such as kangaroo rat mounds

and patches of dominant plants. Field sampling was conducted in September 1997 at the seasonal peak of herbaceous growth.

Transition zone scale. The transition zone from grassland to shrubland was defined based on a decrease in dominance of *L. tridentata* from the south to the north. Trends in plot-scale characteristics across the transition zone were used to assess how the decrease in "dominance" of *L. tridentata* was related to changes in soil texture and the "dominance" of *B. eriopoda*. These two species formed patches in the transition zone, i.e. homogeneous areas with respect to the dominant species where individuals of the dominant species occurred adjacent to each other. Within each plot "dominance" of a given species was defined as the percent area of the plot that was occupied by patches of this species. This is different from % cover, as I considered interspaces between neighboring plants (within the same patch) part of the area dominated by the species of interest. The dominance of *L. tridentata*, *B. eriopoda* and the percent area dominated by neither of these two species was assessed in all 10 m x 10 m plots along the transect. Soil texture of 34 randomly selected plots (out of the 45 plots used for sampling species richness at the intermediate scale [see below]) along the transect was determined by collecting 3 composite soil samples. The soil was sampled from 0-30 cm depth, which in many locations was to the depth of the indurated calcium carbonate layer (caliche). These soil samples were dried and analyzed for soil texture using a hydrometer method (for more details on this method see Chapter 2).

Intermediate scale. Spatial heterogeneity at the intermediate scale within each 10 m x 10 m plot was assessed by the heterogeneity in dominance of the plot and by the intensity of disturbance. The heterogeneity in dominance was calculated from the

dominance estimates in the plots made for the transition zone-scale analysis (for the method of calculation see Analyses). The intensity of disturbance was assessed by classifying each plot into one of six classes based on soil disturbance and the structure (but not the composition) of the vegetation. The structure of the vegetation was considered 'disturbed' when it contained signs of removal of perennial biomass. Both soil disturbance and the structure of the vegetation were taken into consideration for this classification to reflect the combined effect of the burrowing activity of kangaroo rats and other disturbances such as former grazing by domestic livestock. The disturbance classes were defined in the following way: 1= undisturbed, 2= slightly disturbed (5-10% of the plot 'disturbed'), 3= moderately disturbed (15-20% of the plot 'disturbed'), 4= intermediate disturbance (25-30% of the plot 'disturbed'), 5= important disturbance (35-60% of the plot 'disturbed'), 6= strongly disturbed (65-100% of the plot 'disturbed').

Species richness at the plot scale was determined for 45 of 500 10 m x 10 m plots along the transect. These 45 plots were chosen in a random manner with the condition that at least 8 were in each of the following 4 dominance-disturbance classes: (1) low disturbance (disturbance classes 1-4) and low dominance of *L. tridentata* (< 15% of area dominated), (2) low disturbance and high dominance of *L. tridentata* (≥ 15% of area dominated), (3) high disturbance (disturbance classes 5-6) and low dominance of *L. tridentata*, and (4) high disturbance and high dominance of *L. tridentata*.

Plant scale. Variability of dominant plants at the plant scale was described as a patch mosaic of plant canopies and interspaces. Remotely sensed data from the densest stands of the two dominants within the 100 m x 500 m transect were used for this analysis. A dense stand was defined as a patch where dominance was continuous and

cover was highest in comparison to other areas within the transect. Patches that corresponded to these criteria could be found all along the transect for *B. eriopoda*, whereas for *L. tridentata* it could only be found at the shrub dominated end of the transect. Because of the different size of the two dominant species, I used photographs taken from a different height and with different resolution to describe the structure of these selected stands.

For *B. eriopoda*, I used photographs taken from 6 m height with a boom-mounted camera in September of 1997. These photographs covered an area of 3 m x 4 m. Ten photos were taken from evenly placed plots (50 m apart) along the transect. Boundaries of *B. eriopoda* canopy patches (this could include more than one individual, if they had a continuous canopy) on the photos were digitized using ARC/INFO GIS (Geographic Information System). For *L. tridentata*, I used a high resolution (ca. 0.3 m R. Parmenter, pers. comm.) color aerial photo of an area of 60 m x 90 m from the shrub dominated end of the transect taken in June of 1993. The aerial photo was magnified four times and scanned at high resolution (600 dpi). I then used color filters to classify pixels into either shrub or intershrub area, until I reduced the color picture to a black and white mosaic to represent shrubs and intershrub areas. Validation of this mosaic was done by comparing the result to the original photo on which shrubs could be detected visually.

To assess the plant scale species richness, I used the same forty-five 10 m x 10 m plots that I sampled for species richness at the intermediate scale. In each plot, I chose between 0 and 5 *L. tridentata* and *B. eriopoda* individuals (according to the presence and absence of the dominants on the plot) to sample the species richness of subdominant species in microsites around dominant plants. In addition to the two microsites (canopy

and interspace) defined on the photos, I defined a transitional microsite as the canopy edge for each plant. Because of differences in canopy structure between *L. tridentata* and *B. eriopoda*, this transitional microsite had a different width for each lifeform. The *B. eriopoda* canopy edge was defined as the difference between the basal cover and the canopy cover, whereas the *L. tridentata* canopy edge was defined as the area, partly underneath the leaf canopy and partly in the interspace adjacent to the shrubs. The part that was underneath the leaf canopy covered the outer edge of the canopy, where it was mono-layered and discontinuous (Table 3.1). Species richness was assessed in six microsites: grass canopy, grass canopy edge, grass interspace, shrub canopy, shrub canopy edge, and shrub interspace. Plots used to sample these microsites corresponded in size to the area of the microsites and therefore varied in size according to the size of the individual being sampled. I selected this approach in order to include all species growing in these microsites. Furthermore, this method was easily adapted to microsites of very different sizes. For each individual around which microsites were sampled, I noted if there were other individuals of the dominant species immediately adjacent to it or not (i.e. if it was part of a group of plants). This gave me information about the intermediate-scale heterogeneity in dominance around the individual sampled - if it was in a group the heterogeneity was low and vice versa.

III. Analyses.

The spatial variation of ecological variables may have three components: (1) directional trends in the mean (non-stationarity); (2) variation that is correlated between data points at a short distance from each other (spatial autocorrelation), but is assumed to be independent of the location in the gradient; and (3) random variation due to

measurement error and other unexplained sources (Burrough 1995). Classical statistics assume independence between samples, thus the first two components of variation (both indicating spatial dependence of the samples) violate this assumption (Legendre 1993). I first tested each variable used in this study for spatial dependence. If spatial dependence was detected, it was modeled (and thus removed) before combinations of variables were analyzed. A trend along the transect could be removed by regressing the data on the coordinate indicating the position of the plot along the transect - similar to a trend surface analysis, but only in one dimension (Burrough 1995). Spatial autocorrelation can be modeled using a spatial autoregressive model (Cliff and Ord 1981, Reich and Davis 1998).

Table 3.1. The size and shape of the microsites sampled around individuals of the dominant species

Microsite sampled	**Size of microsite sampling plots around *L. tridentata***	**Size of microsite sampling plots around *B. eriopoda***
Canopy	Radius of circular sampling plot is around 75% of the radius of the leaf canopy	Sampling plot corresponds to basal area of plant approximated by an ellipse
Canopy edge	Ring around the leaf canopy edge covering around 25% of the radius of the leaf canopy inside and outside of the leaf canopy	Ring of 3 cm around the edge of the plant
Interspace	3 circular sampling plots with the same radius as the canopy sampling plot. They were situated adjacent to the canopy-edge sampling plot.	3 circular sampling plots, with a radius that corresponded to the minimum(the shorter radius of the canopy sampling plot, the longest radius fitting in the interspace). The plots were situated adjacent to the canopy-edge sampling plot.

Transition zone scale. Variability of system properties at the landscape scale was expressed in terms of their trend across the transition zone. The strength of this trend was tested by calculating Pearson's product moment correlation coefficient (for linear relationships) and Spearman's rank correlation coefficient (for monotonic relationships) between the variable of interest and the coordinate indicating the position of the plot along the transect (Rossi et al. 1992). Species richness was not assessed at the landscape scale since searching for species at this scale would have taken too long. Furthermore, the transect was not replicated and no statistical analyses could have been made using this information.

Intermediate scale. In order to compare species richness to the variability of the system properties of interest, I expressed the variability of these properties within the plots, rather than their variability across the transition zone. Disturbance class was already an expression of the variability in the plots. For the dominant species, I translated the dominance values into an aggregated index of "heterogeneity in dominance" within each plot. The heterogeneity in dominance was expressed using two elements: the number of dominance types observed in each plot, and their evenness. As mentioned above (see Sampling), I distinguished three different types of dominance: dominance by *L. tridentata*, dominance by *B. eriopoda*, and dominance by neither of these two species. A diversity index based on information theory combines the number of dominance types and their evenness into one index (Pielou 1975):

$$H = -\sum_{i=1}^{n} \left(\frac{C(i)}{100} * \ln\left(\frac{C(i)}{100}\right)\right)$$

where H is the heterogeneity in dominance, n is the number of dominance types (n=3), C(i) is the % dominance of type i (Romme 1982). This index does not take into account the spatial arrangement of dominance (i.e., many small patches or one large one). However, if patch shapes are similar along the transect, this is a good measure of the relative spatial heterogeneity in the plots.

The heterogeneity of soil texture at the plot scale could not be described since soil samples from plots were pooled together. However, I was able to determine if the pooled samples from plots located close to each other were more similar to each other than the pooled samples from plots far apart. If this was true, it would indicate there are uniform soil patches that are bigger than the 10 m x 10 m plots. Thus, each plot would only contain one type of soil patch and therefore it could be argued that the plots were homogeneous with regard to soil texture. I tested this hypothesis by calculating the spatial autocorrelation coefficient (Moran's I) for the residuals remaining after removing the trend across the transition zone from the data (Reich and Davis 1998).

I tested whether the heterogeneity in dominance and intensity of disturbance could explain perennial and annual species richness using a regression model (ordinary least square method, [Reich and Davis 1998]). Before using this regression model, I tested if the variables exhibited spatial trends and spatial autocorrelation. Similar methods to relate landscape structures to vegetation pattern have been used in other studies (Stohlgren et al. 1999, Ali et al. 2000).

Plant scale. Variability in dominant plant cover at the plant scale was described by defining canopy and interspace patches and measuring their scale. I used the photos for this purpose. I then analyzed the relationship between species richness and the

defined microsites by comparing species richness among these patches. On the photos, I measured canopy and interspace area of the two dominant species using a GIS. Scale (or patch sizes) of this patch-mosaic was determined by creating a frequency distribution of interspace patch sizes in the matrix of each dominant. I conducted this analysis by imposing a grid with gridcells of a certain size (selected from a range of sizes (0.01 m^2 - 1 m^2) on the digitized landscapes using a GIS. I then classified each gridcell as either plant or interspace depending on the presence or absence of plant canopy in the cell. The percentage of gridcells that was classified as interspace corresponded to the frequency of interspace patches of the defined size (including multiple small patches that resulted from the subdivision of bigger patches). This was subtracted from the percentage of patches that were in the next higher size class to obtain the frequency distribution of interspace patch sizes.

In order to compare species richness of different microsites, I first had to account for the dependence of species richness on sample plot area. This was done using a regression of species richness on area. Based on visual inspection of the scatter plots and a previous finding that the relationship between species number and area is linear at small spatial scales (He and Legendre 1996), I used a linear model to account for area effects on species richness in these microsites. Because there was spatial autocorrelation detected in the residuals of species richness regressed on area, I used a spatial autoregressive model for testing the relationship between microsites and species richness (Cliff and Ord 1981, Reich and Davis 1998). Microsites were introduced into the regression model by creating dummy variables (Ott 1993). The significance of regression coefficients of these dummy variables and of their interaction terms with area

was used to assess if these microsites had a significant influence on species richness (alpha = 0.05).

Comparison across scales. To test if plot-scale heterogeneity was related to plant scale species richness, I used a binary variable associated with plant groups (0 = single individual, 1 = individual within a group of plants) as a covariate in the regression equations explaining species richness at the plant scale.

The landscape-scale variability in shrub dominance could not be described by a linear function along the transect (see Results). It was found that this variability was best modeled by the maxima of shrub dominance in each 10 m along the transect. The values of these maxima were used to determine the significance of overall landscape variability in explaining species richness at the intermediate scale. This variable was added as a covariate into the regression equations explaining species richness at the intermediate scale and the significance of the regression coefficient was tested to determine the relative contribution of landscape variability to vegetation pattern (alpha = 0.05).

Furthermore, I was interested if there were any significant changes in species composition along the transect. In another study the first ordination axis of a Detrended Correspondence Analysis was successfully used to detect ecotones in species composition (Lloyd et al. 2000). I performed a Detrended Correspondence Analysis on annual and perennial species composition separately using the Multi-Variate Statistical Package (MVSP v. 3.12, Kovach Computing Services 2001), and depicted the resulting ordination scores from the 1st axis as a function of position of plots along the transect.

Results

I. Variability of system properties.

Transition zone scale. The maximum value of *L. tridentata* dominance in each 10 m interval decreased across the transition zone, which corresponds to a factor-ceiling distribution (Figure 3.2a). This indicates that a factor varying across the transition zone may be limiting the dominance of *L. tridentata*, but that locally other factors may be more important than this overall limiting factor. Visualization of this distribution was improved by adding a smoothed (over 30 m) line of the maxima of *L. tridentata* dominance along the transect to the graph. This line indicates that there was a sharp decrease in *L. tridentata* dominance between 130 and 190 m, and a second peak in dominance ca. 300 m from the shrubland end of the transect. In comparison, *B. eriopoda* dominance was only weakly correlated with the transition from grassland to shrubland (Figure 3.2b). The variation of soil texture exhibits a clear monotonic but non-linear trend across the transition zone with an inflexion point at about 320 m distance from the shrubland end of the transect (Figure 3.2c). Generally, sand content increased and fine particle content decreased towards the grassland end of the transect. The trend in soil properties was modeled using a second order polynomial function of position along the transect (Table 3.2).

Intermediate scale. Spatial heterogeneity in dominance within plots ranged from 0 - 1.1 with an average of 0.6. This was similar to the 45 plots selected for assessment of species richness, where the spatial heterogeneity in dominance ranged from 0.15 - 1.1 with an average of 0.65. Across the transect, 55 % of the plots were classified as highly disturbed (classes 5 and 6). Similarly amongst the 45 plots sampled for species richness, 51% were classified in these categories.

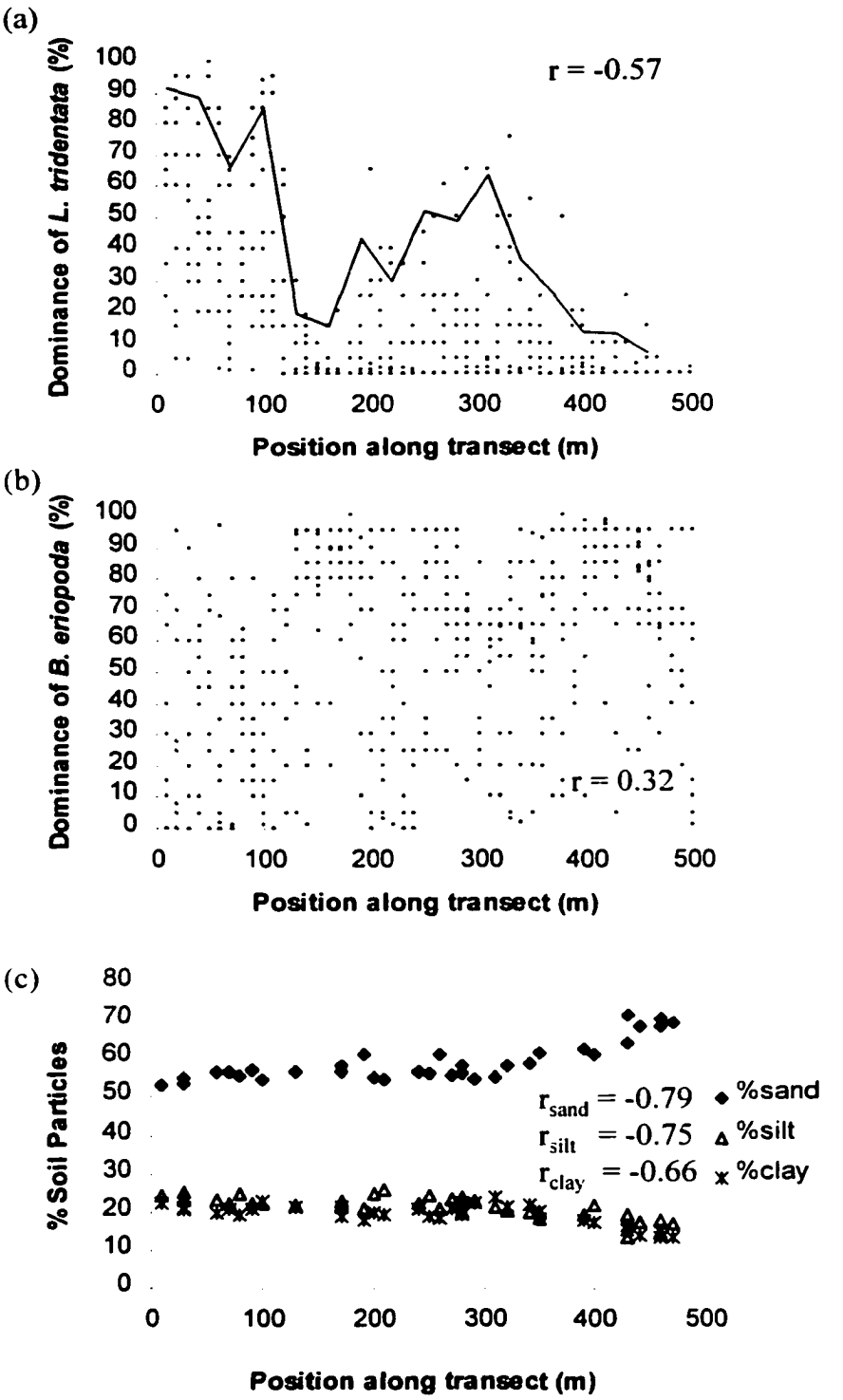

Figure 3. 2. Scatterplots of system properties measured at the plot scale along the transect (from 0 m [shrubland] to 500 m). Correlation between the variables and the position along the transect is indicated by Pearson's correlation coefficient (r). (a) % dominance of *L. tridentata* (b) % dominance of *B. eriopoda* (c) % sand, silt, and clay in soil samples.

After removing the trend in soil variables across the transition zone, there was no spatial autocorrelation in the residuals indicating that differences in values from nearby plots were just as high as from plots far apart (Table 3.2). This suggests that even nearby plots were not located within the same patch of soil and that patches of the soil were likely smaller than the 10 m x 10 m plots. Therefore, soil texture was heterogeneous in these plots.

Plant scale. The canopy to interspace ratio in the patch mosaic formed by the dominant grass (*B. eriopoda*) was very different from the patch mosaic of the dominant shrub (*L. tridentata*) (Figure 3.3). In a dense patch of grass, only 39 % of the area was covered by interspace, and this interspace was divided into small patches that were mostly 1 dm^2 or less in area (Figure 3.3c). In contrast, even in dense shrub stands, 78 % of the area was between shrubs. Furthermore, patches between shrubs were large; 45 % of them were 1 m^2 or more in area (Figure 3.3d).

Table 3.2. Regression equations modelling trends in soil variables across the transition zone, and spatial autocorrelation of the residuals (Moran's I). The variable 'x' designates the distance from the shrubland end of the transect to the plot where the soil sample was collected.

	Regression equation modelling trend across transect			**Test of autocorrelation of the residuals**	
Soil variable	**Equation**	**p-value**	**R^2**	**Moran's I**	**p-value**
% sand	$56.9 - 0.03*x + 0.0001*x^2$	< 0.001	0.80	-0.01	0.46
% silt	$23.2 + 0.009*x - 0.0001*x^2$	< 0.001	0.71	-0.05	0.79
% clay	$19.9 + 0.021*x - 0.0001*x^2$	< 0.001	0.67	0.06	0.10

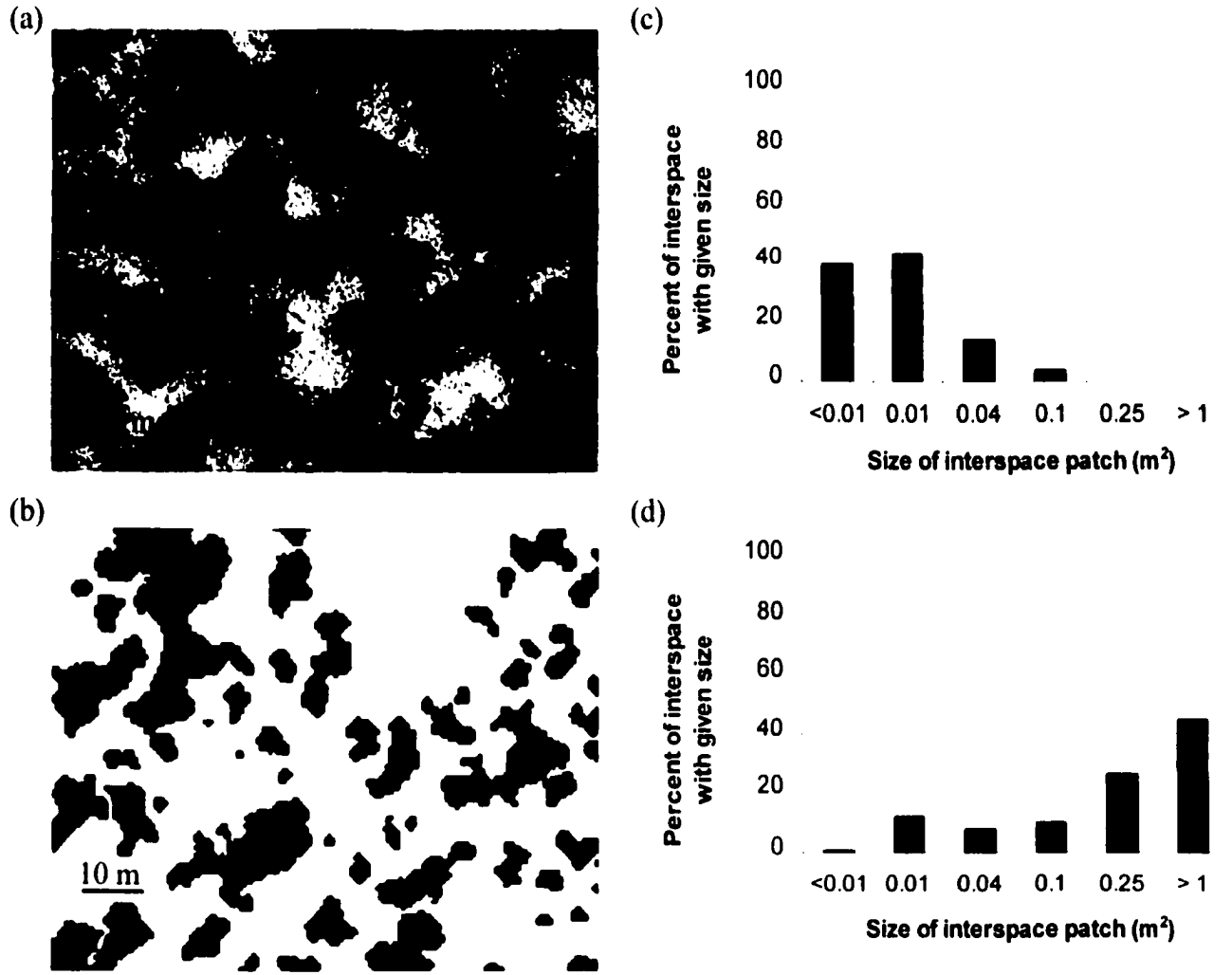

Figure 3.3. Patch-matrix structure of dominant species as digitized from photographs (left). (a) the structure created by the presence of *B. eriopoda* (b) the structure created by the presence of *L. tridentata*. Interspace patch size frequency distribution (right) (c) in *B. eriopoda* matrix (d) in *L. tridentata* matrix.

II. Relationship between species richness and variability in system properties.

Intermediate scale. Preliminary analyses showed that variables at the plot scale did not exhibit any spatial trend across the transect, nor any spatial autocorrelation, thus samples were independent. The relationship between perennial species richness and heterogeneity in dominance (H) was significant, with an increase in richness as heterogeneity in dominance increased (Figure 3.4a). Annual species richness was linearly related to spatial heterogeneity in dominance (H) and to disturbance class, although richness was more closely related to disturbance class than to spatial heterogeneity in dominance (Figure 3.4c,d). Disturbance class explained 34 % of the variation in annual species richness, whereas the spatial heterogeneity of dominance explained only 27%. The variability of the two system properties combined explained 39% of the variation in species richness (not shown).

Plant scale. No trend across the transect was found in the plant scale data. Because there was spatial autocorrelation, I used an autoregressive model for the analyses of these data (Cliff and Ord 1981, Reich and Davis 1998). Since sample plots for this scale were of variable size, species richness was explained by the size of the sample plot and the type of microsite. The importance of area for explaining species richness varied with the dominant species around which microsites were sampled. Around *L. tridentata*, 45 % and 47 % (for perennials and annuals) of the variation in species richness was modeled by the size of the sample plot, whereas around *B. eriopoda* only 11 % and 17 % of this variation was due to area sampled in microsites (not shown).

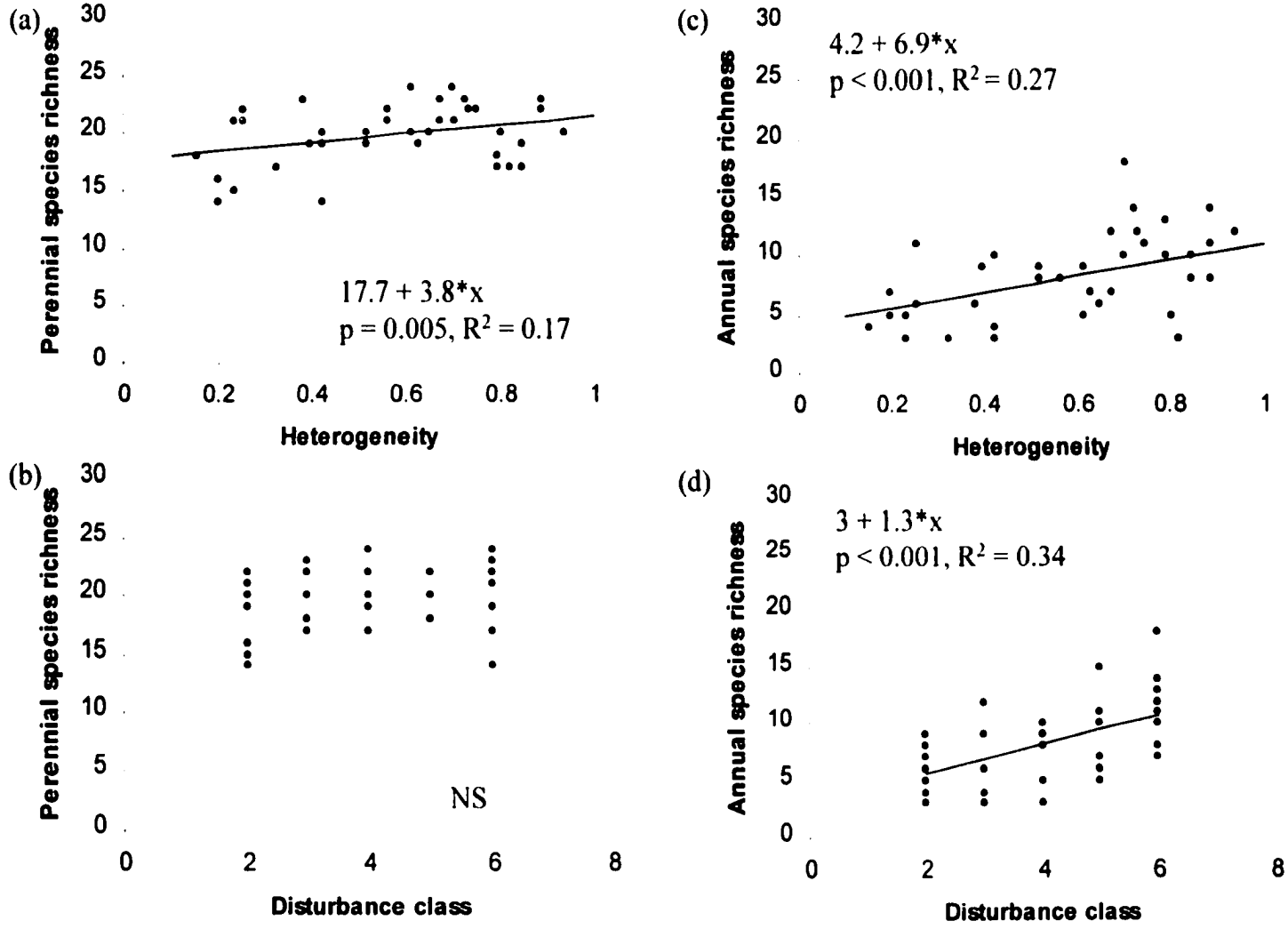

Figure 3.4. Species richness with landscape heterogeneity at the meso scale. (a) Perennial and (b) annual species richness versus spatial heterogeneity in dominance (c) Perennial and (d) annual species richness versus disturbance class

Using the type of microsite as an additional explanatory variable, I discovered that around *B. eriopoda* species richness was not dependent on area in two microsites (grass canopy and canopy edge). This contributed to the improvement of the models explaining the variation of annual and perennial species richness in microsites; 14 % more could be explained for microsites around grasses and 4 % - 5 % for microsites around shrubs (Table 3.3). For perennial species, the improvement of the model when adding a distinction between microsites was related to both differences in the intercept and in the slope of the relationship between species richness and area. However, it was not clear in which microsite perennial species richness was highest, since slope and intercept of the species-area relationship varied in sometimes opposite directions between microsites. In comparison, for annual species only the slope of the species-area relationship changed among microsites. Among shrub microsites, it was smaller in the canopy and canopy edge than in the interspace, suggesting that annual species richness was highest in the interspace. These species-area relationships should not be used for extrapolation much beyond the scale of the samples, as the slopes may change as area increases.

Table 3.3. Importance of the distinction between microsites for plant scale species richness. The best fitting linear model (species richness = intercept + (slope) * area) is shown. '0' coefficient indicates a non-significant contribution of the explanatory variable to the model. Different letters indicate that interaction terms between 'Microsite' and intercept or slope were significant (i.e. these coefficients were significantly different between microsites).

Response variable	Microsite	Intercept (p-value)	Slope (p-value)	p-value of model	R^2 of model
Perennial species richness	*B. eriopoda* canopy	0.16 (0.003) A	0 A		
	B. eriopoda canopy edge	0.53 (< 0.001) B	0 A		
	B. eriopoda interspace	0.16 (0.003) A	6.9 (< 0.001) B	(< 0.001)	0.25
Annual species richness	*B. eriopoda* canopy	0.006 (0.91) A	0 A		
	B. eriopoda canopy edge	0.006 (0.91) A	0 A		
	B. eriopoda interspace	0.006 (0.91) A	5.3 (< 0.001) B	(< 0.001)	0.31
Perennial species richness	*L. tridentata* canopy	2.1 (< 0.001) B	2.1 (< 0.001) B		
	L. tridentata canopy edge	3.2 (< 0.001) C	1.1 (< 0.001) A		
	L. tridentata interspace	1.5 (< 0.001) A	2.1 (< 0.001) B	(< 0.001)	0.50
Annual species richness	*L. tridentata* canopy	0.34 (0.76) A	0.86 (< 0.001) A		
	L. tridentata canopy edge	0.34 (0.76) A	0.86 (< 0.001) A		
	L. tridentata interspace	0.34 (0.76) A	1.8 (< 0.001) B	(< 0.001)	0.51

III. Comparison across scales.

Plant to the plot scale. The regression coefficient for the covariate indicating if the sampled individual occurred in a group or not was significant in four out of the six microsites (Table 3.4). However, only small percentages (1-2 %) of the total variation in small-scale species richness could be explained by this variable (compare Tables 3.3 and 3.4). Species richness was smaller in the interspace of grasses and the canopy area of the shrubs when a plant was in a group of grasses or shrubs (Table 3.4), whereas it was larger in interspaces between shrubs in a group. Therefore, the influence of this intermediate-scale variable depended on the microsite sampled, which indicates that smaller scale landscape structures can modify the influence of larger scale factors.

Plot scale to the transition zone scale. Variability at the landscape scale was expressed as a trend in the maxima of *L. tridentata* dominance across the transect. The change in these maxima did not explain variability in annual or perennial species richness since regression coefficients for this variable were non-significant (not shown). This is not surprising since there was a poor visual fit of the smoothed line of the maxima of shrub dominance along the transect and variability in species richness (Figure 3.5a,b). In contrast, perennial species composition showed a trend along the transect, as expressed by the position of the plots on the first ordination axis (Figure 3.5c). This trend was similar to the decrease in shrub dominance. This shows that the change in perennial species composition could be due to the change in overall shrub dominance along the transect, or factors that are likely correlated with this, such as variation in soil texture (Figure 3.2c). Annual species composition did not exhibit trends - as expressed by the first ordination axis - along the transect (Figure 3.5d).

Table 3.4. Relationship of plant scale species richness and spatial heterogeneity at both the plant and the plot scale. Best fitting linear model is shown. Explanatory variables with '0' coefficient did not have a significant contribution to the model. Different letters indicate that interaction terms between 'Microsite' and other explanatory variables were significant.

Response variable	Microsite	Intercept (p-value)	Coefficient for area (p-value)	Coefficient for group (p-value)	p-value of model	R^2 of model
Perennial species richness	*B. eriopoda* canopy	0.24 (< 0.001)	0	0		
		A	A	A		
	B. eriopoda canopy edge	0.53 (< 0.001)	0	0		
		B	A	A		
	B. eriopoda interspace	0.24 (< 0.001)	7.5 (< 0.001)	-0.28 (< 0.001)	(< 0.001)	0.27
		A	B	B		
Annual species richness	*B. eriopoda* canopy	0.04 (0.46)	0	0		
		A	A	A		
	B. eriopoda canopy edge	0.04 (0.46)	0	0		
		A	A	A		
	B. eriopoda interspace	0.04 (0.46)	6.1 (< 0.001)	-0.23 (< 0.001)	(< 0.001)	0.33
		A	B	B		
Perennial species richness	*L. tridentata* canopy	2.5 (< 0.001)	2.1 (< 0.001)	-0.84 (< 0.001)		
		B	B	A		
	L. tridentata canopy edge	3.7 (< 0.001)	1.1 (< 0.001)	-0.84 (< 0.001)		
		C	A	A		
	L. tridentata interspace	1.5 (< 0.001)	2.1 (< 0.001)	0.14 (< 0.001)	(< 0.001)	0.51
		A	B	B		
Annual species richness	*L. tridentata* canopy	0.53 (0.45)	1.0 (< 0.001)	0		
		A	A	A		
	L. tridentata canopy edge	0.53 (0.45)	1.0 (< 0.001)	1.2 (< 0.001)		
		A	A	B		
	L. tridentata interspace	0.53 (0.45)	1.6 (< 0.001)	1.0 (< 0.001)	(< 0.001)	0.53
		A	B	B		

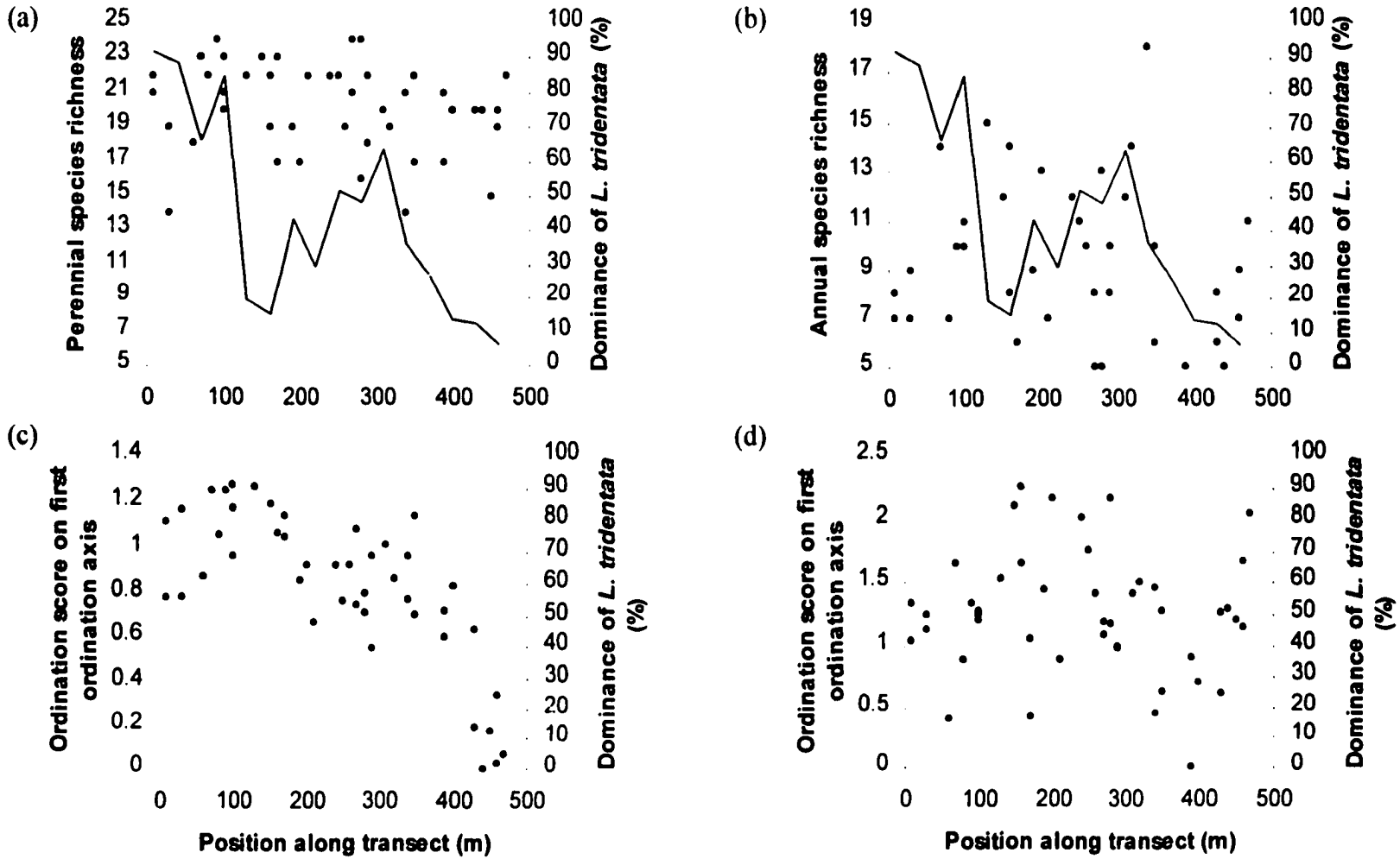

Figure 3.5. Species richness and composition along the transect. (a) perennial species richness (b) annual species richness (c) perennial species composition (d) annual species composition. Points represent data for species richness, and the position of the plots on the 1st ordination axis for species composition. The line corresponds to a smoothed line of the maximum dominance of *L. tridentata* along the transect.

To summarize the results, correspondence between species richness (or composition) and heterogeneity of system properties was found at all scales investigated (Table 3.5). At the plant scale, the highest correspondence was found with area of microsites around shrubs, and patch types around grasses. At the plot scale, disturbance class explained annual species richness best. At the landscape scale, the change in shrub dominance across the transition zone was related to changes in perennial species composition. Therefore, the strength of the relationship between system properties and species richness varied according to the functional group, system property, and scale investigated.

Table 3.5. Summary of results. -- indicates interactions not measured and NS indicates non-significant interactions.

Scale	**Species richness of**	**Percent of variability in species richness explained by**		
		Area	**Environmental conditions (soil texture, dominant plants)**	**Distur-bance**
Transition zone scale	Perennials	--	Change in species composition	--
	Annuals	--	NS	--
Intermediate scale	Perennials	--	17 %	NS
	Annuals	--	27 %	34 %
Plant scale (around shrubs)	Perennials	45 %	5 %	--
	Annuals	47 %	4 %	--
Plant scale (around grasses)	Perennials	11 %	14 %	--
	Annuals	17 %	14 %	--

Discussion

Species richness is a response variable that combines the reaction of multiple species into an index of the overall heterogeneity of the vegetation (Kolasa and Rollo 1991). Since the distribution of plant species is closely related to ecosystem properties, such as environmental conditions and intensity of disturbance, a good correspondence between the variability of ecosystem properties and species richness has been repeatedly observed (Rosenzweig 1995). The results from this study correspond well to this general finding. Following my three specific objectives I will first discuss the variability of system properties, second the relationship between their variability and species richness, and third the cross-scale comparison of species richness and heterogeneity.

I. Variability in system properties.

The pattern of *L. tridentata* dominance across the transition zone was not gradual, but rather exhibited several discontinuities. The distribution of plant species at ecotones is likely governed by the interplay of many different factors (Grover and Musick 1990, Richardson and Bond 1991). Strong resource limitation of plant species in arid environments generally leads to a good correspondence of soil characteristics with plant distributions (Gosz and Sharpe 1989). This is supported by the observation that one of the decrease of *L. tridentata* dominance at the grassland end of the transect coincided with a change in soil texture. However, biotic factors - most importantly seed availability - may also have contributed to the distribution patterns of *L. tridentata* (Richardson and Bond 1991, Malanson 1997). It has been observed that encroachment of *L. tridentata* into desert grasslands proceeds from a few pioneer individuals which increase seed availability and facilitate growth of seedlings around them (Gardner 1951). This pattern

of expansion leads to a clumped distribution of individuals at the transition between shrublands and grasslands that could explain the second peak of dominance observed along the transect.

The landscape scale variability in shrub dominance did not seem to have any influence on small- and intermediate-scale heterogeneity since no trends were detected in those variables along the transect. This somewhat surprising result illustrates the dependence of the heterogeneity perceived on the response variable and scale of observation (Kolasa and Rollo 1991). When the response variable (heterogeneity in dominance instead of dominance) or the scale of observation (microsites instead of gradient across transition zone) was changed, the landscape boundaries were no longer detected. Similarly, in another study it was found that the larger the sample plot, the more clearly landscape boundaries could be perceived, whereas the between sample variance at smaller scale was so high that boundaries could not be detected (Rescia et al. 1997).

Soil texture data indicated that soil samples from single plots should not have been pooled, since plots most likely were heterogeneous with regard to soil texture. In another study at the same site, it was found that soil texture was even more variable than the cover of dominant plants (Bestelmeyer 2000). This needs further investigation since soil texture variation at ecotones may be an important factor determining species distributions (Gosz and Sharpe 1989, Kröel-Dulay et al. submitted). At the plant scale, the cover of *L. tridentata* corresponded to estimates from the literature (Wierenga et al. 1987, Johnson, A. R. et al. 2000). However, the cover of *B. eriopoda* was high in comparison with other estimates (Johnson, A. R. et al. 2000, Hochstrasser et al.

submitted). This is likely due to exceptionally good soil conditions in the study area (in comparison to other areas at the same site) and a climatically favorable year, since cover of dominant grasses can vary with weather at this site (Gosz 1993).

The spatial heterogeneity detected in this study was only a shapshot in time that may change over time. For example, there was an increase in the presence of shrubs over the past century (Gardner 1951). However, this shrub encroachment is generally believed to be discontinuous in time and related to threshold behavior of these systems (van de Koppel et al. 1997). Once the change has occurred, the longevity of shrubs creates a relatively slow changing system, that maintains the relative abundance of plant species and their the distribution over time (Cody 2000). Some disturbance patches, such as kangaroo rat mounds persist over a long time, as animals continue to occupy them or reoccupy them periodically (Chew and Whitford 1992). Therefore, even though this study can be considered a shapshot in time, some fundamental characteristics of the structure of this transition zone may have been captured.

II. Relationship between species richness and variability in system properties.

A hierarchical structuring of system properties to relate them to species richness has been proposed (Urban et al. 1987, Kotliar and Wiens 1990, Gosz 1993). However, I found that dominant plants had an influence on species richness across multiple scales at this transition zone. This contributes to repeated evidence that important system properties, such as variation in soil texture, dominance of the vegetation and disturbance, may exhibit a multi-scale structure that cannot easily be decomposed into discrete hierarchically ordered factors influencing species richness (Collins and Barber 1985, Kotliar 1996). Furthermore, even though the system properties remain the same across

scales, different processes may be the cause of their influence on species richness at each scale. For example, whereas plant competition may be important for the species richness in microsites around dominant plants, changes in abiotic factors associated with groups of dominant plants maybe more important in and around these groups (Briones et al. 1998, Ludwig et al. 2000, Novoplansky and Goldberg 2001).

Results from this study illustrate the difficulty in recognizing and defining all the factors that are contributing to species richness at any given scale. At the plant scale, I could explain 4-14 % of the variation of species richness by the recognized patch structure, and 17-39 % of the variation in species richness by heterogeneity of defined factors at the plot scale. The amount of variation in species richness modeled in this study is similar to other studies relating plant species diversity to defined factors - or their variability. Generally only less than 50 % of the variation in species richness could be accounted for (Gibson and Hulbert 1987, Linder 1991, Stohlgren et al. 1999, Ali et al. 2000). Only studies that included 'area' as an explanatory variable could model high percentages of the variation in species richness (Johnson, M. P. et al. 1968, Harner and Harper 1976). However, the variable 'area' includes unexplained spatial heterogeneity caused by a combination of factors at multiple scales and is therefore a poor explanatory variable. I found evidence for this kind of unexplained variation in the microsites around shrubs, since species richness was strongly dependent on the area of these sites. If factors explaining species richness are recognized, however, the relative success in explaining variation in species richness at the plot scale suggests that system properties are best described in terms of their variability. This is not surprising as species richness can be considered a system property that measures the heterogeneity of the vegetation.

Annual and perennial species differed in their responses to environmental heterogeneity at this transition zone. Whereas perennial species composition was sensitive to overall changes in shrub dominance across the transition zone, annual species composition did not change. However, at the plant and plot scale annual species richness was more dependent on variation in system properties than perennial species richness. These differences between annual and perennial species may be related to the different responses of these functional groups to environmental conditions. Whereas the occurrence of perennial plant species is a cumulative response over time, annual species respond opportunistically to conditions in the year of sampling (Bowers 1987). In some years - as it was the case for this study (unpublished data)- sufficient levels of soil moisture for the germination of annuals may only be available in certain microsites (Gutierrez and Whitford 1987). The different response to system properties of these functional groups suggests that because of the individualistic response of species to environmental factors, it may be necessary to study the response of specific species to certain system properties rather than the aggregated response of all species at a site. However, even in this case, factors operating at multiple levels may make it difficult to establish a causal correlation between the environment and the spatial distribution of certain species (Kotliar 1996). It seems that ecologists are still falling short of being able to establish a close relationship between pattern and process (Moloney 1993).

III. Cross-scale comparison.

Landscape factors measured at larger scales than the scale of measurement of species richness could only explain a small fraction of the variation in species richness and their effect was modified by smaller scale landscape structures. This suggests that

mainly local processes influence species richness and that the context of the sample is not as important (Huston 1999). A similar result was found in a study of human influenced landscapes in northern Spain (Rescia et al. 1997). The importance of small-scale processes for creating and maintaining vegetation patterns has been emphasized (Grubb 1977, Tilman and Pacala 1993, Huston 1999), and larger scale factors, such as fluctuations in climate, have been shown to alter these processes - thus indirectly affecting species coexistence patterns (e.g. Richardson and Bond 1991, Briones et al. 1998).

Nevertheless these indirect effects of intermediate-scale factors were important in explaining plot-scale species richness at this transition zone. Therefore, sampling at the plot scale was useful in that it helped relate the plant to the scale of the transition zone. Even though perennial and annual species were sensitive to dominant plants at both the plant and the plot scale, annuals were even more sensitive to disturbance, which was not taken into account at the smaller scale. If extrapolation of local species richness to the landscape scale is desired, constructing a species area curve taking into consideration intermediate-scale heterogeneity seems to be the most reliable method (Weiher 1999). This can be done by combining field data with remote sensing and taking into account species overlap between habitat types (Stohlgren et al. 1997).

Summary and Conclusions

The desert grassland-shrubland transition zone investigated in this study was defined by a non-linear decrease in shrub dominance. Variability of system properties at smaller scale did not change across the transition zone. Species richness was positively related to variability in system properties at all scales. However, there were differences

between functional groups. Whereas annual species richness was more responsive to system properties than perennial species richness at the plant and the plot scale, perennial species composition changed at the scale of the transition zone. In any case, the heterogeneity described at each scale could only explain less than 50 % of the variation in species richness indicating that not all the factors influencing species richness at this transition zone were identified. The observation scale of system properties was also important since the response of species richness to variability in system properties measured at the same scale was stronger than the response to variables describing the larger context of the samples.

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IV. COMPETITIVE DOMINANCE OF TWO LIFEFORMS (SHRUBS AND GRASSES) AND THEIR INFLUENCE ON FUNCTIONAL GROUP COMPOSITION OF THE VEGETATION AT A DESERT GRASSLAND-SHRUBLAND TRANSITION ZONE: A SIMULATION STUDY.

Introduction

Dominant plant species are important elements of the biotic structure of ecosystems and they influence ecosystem dynamics (Lawton 1994, Sala et al. 1996). A change in the dominant species can induce processes that alter the abiotic structure of ecosystems as well as the biotic one (Wilson, and Agnew 1992). Over the past century, shrub encroachment into desert grasslands has occurred in the Southwestern United States (Van Auken 2000). In the northern Chihuahuan desert, many grassland areas formerly dominated by black grama (*Bouteloua eriopoda* [Torr.] Torr.) have been encroached upon by creosotebush (*Larrea tridentata* [Sessé & Moc. ex DC.] Coville) (Gardner 1951, Grover and Musick 1990). This change in the dominant lifeform has altered both the biotic and abiotic structure of these grasslands (Schlesinger et al. 1990, Whitford et al. 2001). The implications of this change in structure for subdominant species composition and diversity have only been investigated using pattern analysis (Chapters 2 and 3). I provide the first mechanistic analysis investigating biotic and abiotic processes that change during shrub encroachment.

The change in the biotic structure of these grasslands occurs because of the differences in morphological, phenological and life history characteristics of black grama (*B. eriopoda*) and creosotebush (*L. tridentata*). Morphological differences between these two species are found in canopy structure and root distribution. The canopy of

creosotebush forms another vegetation layer above surrounding plants, whereas the canopy of black grama occupies the same space as subdominant plants (Belsky 1994). Differences in root distribution between these two dominants are less obvious. It has often been proposed that shrub roots explore soil water resources at greater depths than grass roots (Walker and Noy-Meir 1982, Sala et al. 1997). However, roots of plants tend only to occur where water is available (Caldwell and Richards 1986). In Chihuahuan desert grasslands, most precipitation falls during the monsoon season in summer, when grasses are active and deep percolation of water into the soil is not very likely (Conley et al. 1992). Furthermore, in many areas an indurated calcium carbonate layer (caliche) impedes water flow and root growth to deep layers (Shreve and Mallery 1933). As a consequence, the root system of creosotebush is often relatively shallow and occupies the same soil layers as the roots of black grama (Reynolds et al. 1997). However, root systems of shrubs also differ from root systems of grasses in their intensity, coarseness and expanse (Wilson, S. D. 1998). Whereas the root system of creosotebush is extensive, relatively coarse, and widespread around its canopy, black grama has fine roots concentrated beneath the canopy (Gile et al. 1998, Gibbens and Lenz in press).

Life history and phenological differences between the two lifeforms are pronounced. Creosotebush is long-lived (> 100 years), whereas black grama was found to have a medium lifespan (ca. 40 years) (Nelson 1934, Valentine and Gerard 1969). Establishment from seeds is rare in both species, but black grama spreads vigorously from stolons (Nelson 1934, Valentine and Gerard 1969). Black grama seeds are wind dispersed, whereas the seeds of creosotebush do not have adaptations for a defined dispersal mechanism and tend to accumulate around parent shrubs (Chew and Chew

1965, Boyd and Brum 1983). Water use of creosotebush, an evergreen C3 species, is very opportunistic in time, whereas black grama (*B. eriopoda*), a C4 species, actively grows only during the monsoon season between mid July and October (Kemp 1983, Reynolds 1986). The implications of some of these differences for dominance of these two species in desert grasslands under different climate scenarios have been explored in a previous modelling study (Peters submitted). However, a detailed analysis as to how each of these species comes to dominate desert grasslands, and how, if at all, subdominant species composition changes with a change in the dominant lifeform, has not been conducted.

The change in the dominant lifeform also leads to changes, via feedback loops, in the abiotic structure of the environment. Black grama plants retain large amounts of standing dead biomass in their canopy that can prevent evaporation (Hochstrasser and Coffin, 1997, Gosz, and Gosz 1996). Shading underneath the canopy of creosotebush leads to a microclimatic temperature change in this microsite (Reynolds et al. 1997, Breshears et al. 1998). Since both biotic and abiotic structural changes occur simultaneously during shrub encroachment, the implications of these abiotic feedback loops for subdominant functional group composition are difficult to study in the field. Modelling is a useful tool for separating potential mechanisms that could influence subdominant species composition (Reynolds et al. 1997).

Gap dynamics models are based on demographic processes and are therefore ideal for modelling changes induced by different demographic processes of dominant species (Coffin and Urban 1993, Kobe 1996, Peters and Herrick 2001, Peters submitted). Whereas in mesic environments competition for light is important for vegetation

dynamics, in semi-arid and arid environments competition for belowground resources is more important (Coffin and Urban 1993, Holmgren et al. 1997). The overriding significance of water limitation in these environments is illustrated in studies showing that the positive effect of shading underneath shrubs on water availability outweighs the negative effect of light limitation (Holmgren et al. 1997, Breshears et al. 1998). Therefore, contrary to gap dynamics models of forests, which are based on competition for light, gap dynamics models of semi-arid and arid environments are based on competition for soil water (Coffin and Urban 1993). For this study, I used a gap dynamics model created for semi-arid and arid environments: ECOTONE (Peters submitted). This model (and its predecessor, STEPPE) has been used to evaluate changes in species coexistence patterns of grasslands and shrublands with regard to changes in climate and disturbance in previous studies (Coffin and Lauenroth 1990, Peters submitted). However, changes of functional group composition in reaction to dominant species have not been evaluated using this model.

The objective of this study was to evaluate the influence of biotic differences between black grama and creosotebush - and changes in the abiotic environment induced by these species - on subdominant functional group composition. This general objective can be subdivided into three specific objectives. First, I evaluated the influence on subdominants of biotic differences between the two dominants. Second, the abiotic influence of each dominant on subdominants was investigated. Third, the combined effect on subdominants of the two dominants was simulated to represent the areas where black grama and creosotebush coexist under current climatic conditions (Peters submitted). In addition, modelling results on the relative abundance of these dominants

and the subdominant functional groups were verified by comparing the results to field observations at a grassland - shrubland transition zone.

Methods

I. Site description

Field observations were conducted at and the simulation model was parameterized for the Sevilleta Long-Term Ecological Research (LTER) site (http://sevilleta.unm.edu) situated in central New Mexico (latitude: 34°21'N; longitude: 106°53'W; 1650 m ASL). This site is located in the transition zone between Great Plains grassland, Great Basin shrubland and Chihuahuan desert (Gosz 1992). Long-term (1916-1995) average temperature at a nearby weather station in Socorro, NM ranges from 2.6°C in January to 24.6°C in July; mean precipitation is 232 (± 79 SD) mm (Hochstrasser et al. submitted). The soil texture of McKenzie Flats, an area supporting both Great Plains and Chihuahuan desert grassland, varies between sandy loams and loamy sands (Johnson 1988). Net primary production of the site is estimated at about 193 $g/m^2/yr$ (± 50 SD) (D. Moore, pers. com.). Domestic livestock has been excluded from this site since 1973 but native herbivores, such as jackrabbits and pronghorn antelope, are still lightly to moderately grazing the site. Disturbance caused by the burrowing activity of kangaroo rats (*Dipodomys spectabilis*) is important at this site (Fields et al. 1999).

II. Model description

ECOTONE is a gap-dynamics model developed for simulating vegetation dynamics of grasslands and shrublands in arid and semi-arid areas (Peters and Herrick 2001, Peters submitted). The model contains a tipping bucket soil water model (SOILWAT, [Parton 1978]). In ECOTONE, the relative abundance of species or

functional groups over time is determined through differences in seed dispersal, recruitment, growth and mortality among these groups (Figure 4.1). Water availability and temperature as well as disturbance influence these processes. Even though competition for water may only occur during periods of resource abundance, it is important for shaping species coexistence patterns in arid environments (Fowler 1986, Briones et al. 1998). In the model, plants compete for water based on their root distribution, their fine root to coarse root biomass ratio, and their phenological activity. Water availability per soil layer is determined using the soil water model (Figure 4.1). Soil water and temperature conditions appropriate for germination and establishment of species can also be determined using the soil water model (Minnick and Coffin1999, Peters 2000). Whereas water dynamics are calculated with a daily time step, competition for available water occurs on a monthly basis and growth and mortality of plants on a yearly basis. The differences between these temporal resolutions of processes in the model were necessary since water dynamics can only be accurately simulated with high temporal resolution (Parton et al. 1998), whereas low temporal resolution is sufficient for simulating vegetation dynamics (Peters submitted).

III. Modifications to the previous version of the model

A few modifications to the previous version of the model had to be made for this simulation study. These modifications made recruitment dependent on abiotic conditions, enhanced the plant-soil feedback loop, strengthened the competition, and allowed modification of standing dead biomass in black grama and shading underneath shrub canopies.

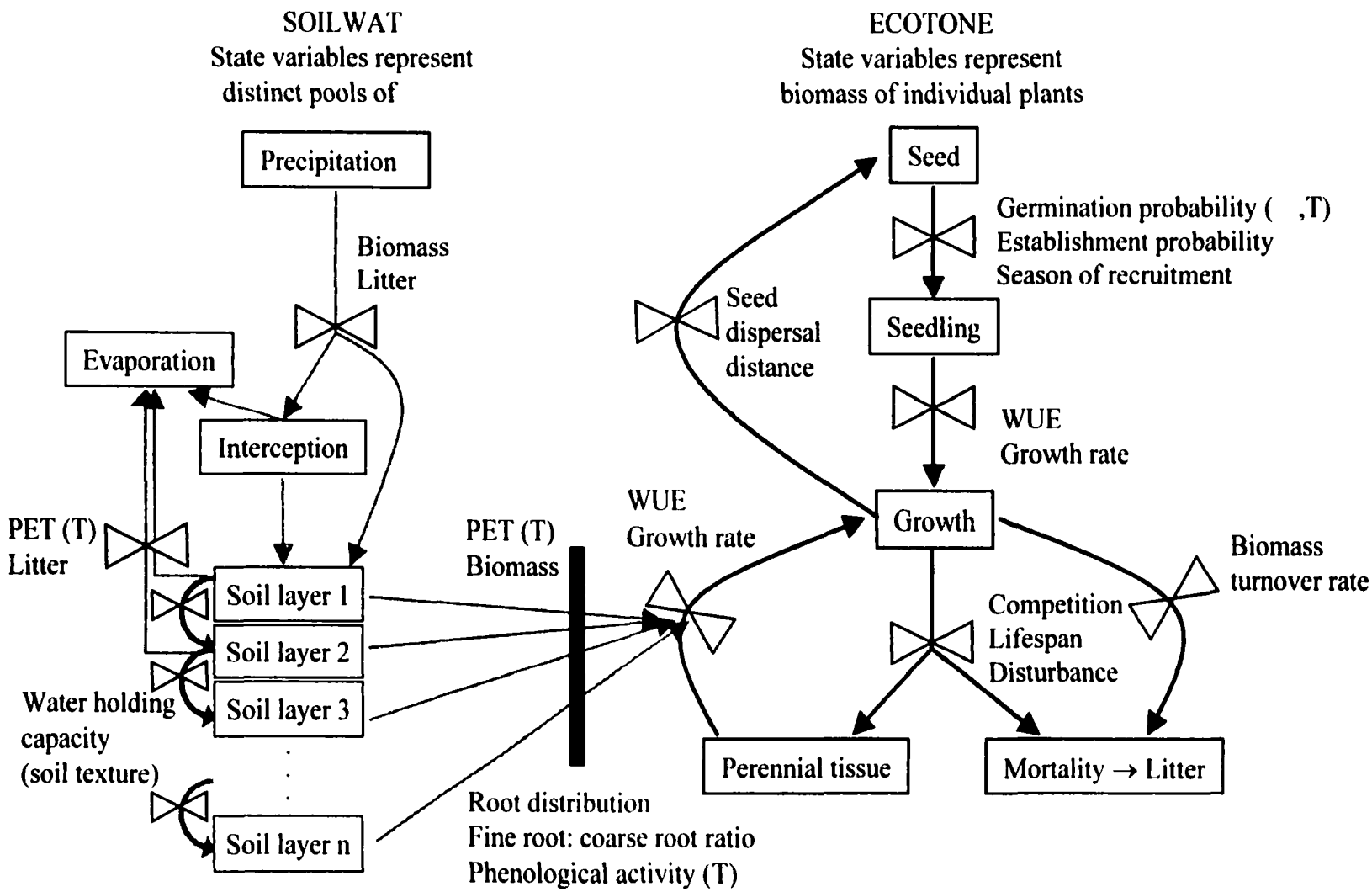

Figure 4.1. Flow diagram of ECOTONE. Grey arrows indicate flows of , black arrows indicate flows of biomass. Available water for plant growth depends both on climate (precipitation, temperature, PET) as well as on species characteristics (bar between SOILWAT and ECOTONE). I indicated in parentheses after control variables if they were dependent on water (W) or temperature (T).

Recruitment. I made changes in the recruitment of plants and in the effect of total biomass and litter on transpiration. In addition to establishment probability and seed availability, recruitment is now dependent on germination probability. The germination probability of a species depends on its germination period during the year and the number of days with appropriate conditions for germination during this period. C3 species have a higher probability to germinate before May 1 and after September 1, whereas C4 species preferentially germinate between May 1 and August 31. The days with appropriate soil water availability and temperature are determined by SOILWAT. Water and temperature conditions necessary for germination are user defined; they are based on the minimum conditions necessary for all species and functional groups modeled. Once the germination probability of each species has been determined using these criteria, germination probability in combination with establishment probability and seed availability determine the chances of recruitment for each species during each recruitment event (Figure 4.1). The actual species recruited is determined stochastically, based on the relative chances of each species to be recruited.

Plant-soil feedback loops. SOILWAT uses the anticipated growth of the plants and litter to calculate available water for plants every year. In previous versions of the model anticipated growth and litter were user defined constants. I modified the model such that this anticipated growth depends on the current biomass on each plot and on the anticipated precipitation for the next year. Next year's precipitation is known in the model, since the precipitation is read from input data files. Litter on the plot is also variable depending on the biomass of plants that have died on the plot and on turnover of aboveground biomass (Figure 4.1). Total biomass (current biomass and anticipated

growth for next year) and litter are used to classify each plot into one of 20 aboveground biomass production classes. SOILWAT calculates available water for each of these production classes, and this information is then used to produce actual growth of plants during the year. Since this feedback loop allows different plots in the simulated landscape to be classified into different production classes, SOILWAT could simulate the differences in abiotic conditions between plots with higher litter, because of the presence of black grama, and control plots.

Competition. As in the original model, competition between plants on the same plot occurs according to their root biomass in each soil layer and their phenological activity (Peters submitted). Perennials take up water necessary for the maintenance of perennial biomass first. The rest of the available water is distributed between perennials and annuals according to their root biomass in each soil layer and their phenological activity. I added a function to the model that does not allow small plants to take up any water when water is limited. Thus, smaller plants can be outcompeted by larger ones. This reflects the stronger competitive abilities of larger plants.

Temperature. I introduced a function that can change the temperature in a given plot when creosotebush is sufficiently large to shade the plot. A change in temperature affects the phenological activity of plants and their germination probabilities (Figure 4.1). The change in temperature induced by shading was simulated according to a function that imitates measured changes in temperature underneath juniper canopies (Breshears et al. 1998):

$$\text{tempadd} = \sin((\text{jdy}-81)*0.017)*\text{par(jdy)})$$

where par(jdy) = 0 if jdy < 81 or jdy > 261,
par(jdy) = 2 if 80 < jdy < 161,
par(jdy) = 4 if 160 < jdy < 262

tempadd is the change in temperature in interspaces between shrubs, jdy is the Julian day of the year and par(jdy) is a parameter that varies over the year depending on jdy. The change in temperature can be negative or positive (Figure 4.2), because the measurements from the juniper woodland showed that in comparison with the average air temperature (measured at 2 m height), the temperature in interspaces is more extreme. In contrast, the temperature underneath canopies corresponds to the air temperature.

IV. Input and parameterization of the model

Daily maximum and minimum temperature as well as precipitation measurements for 65 years (1931 - 1995) were obtained from Socorro, NM. The soil was parameterized to correspond to soil texture found underneath plants at a grassland-shrubland transition zone at the Sevilleta LTER (Chapters 2 and 3). The soil profile used was a sandy loam with a loamy sand topsoil (0-5 cm was 8 % clay and 75 % sand, 5-10 cm was 10 % clay and 70 % sand, 10-15 cm was 15 % clay and 65 % sand, and 30-75 cm was 20 % clay and 60 % sand). This soil texture can sustain both dominants. Small scale disturbances affecting single plots occurred at low frequency ($p = 0.055$) during the simulation.

Species characteristics. Dominant species and subdominant functional group characteristics were defined based on data from the literature (Peters submitted). A good review of arid land plant characteristics can be found in (MacMahon and Schimpf 1981). Changes from (Peters submitted) were made due to a slightly modified input structure of the model and additional information found in the literature about species characteristics as well as field observations (Table 4.1). The adjustments made were:

- An increase in the maximum lifespan of C3 perennial grasses to match the lifespan of C4 perennial grasses, as I had no evidence for different lifespans of these

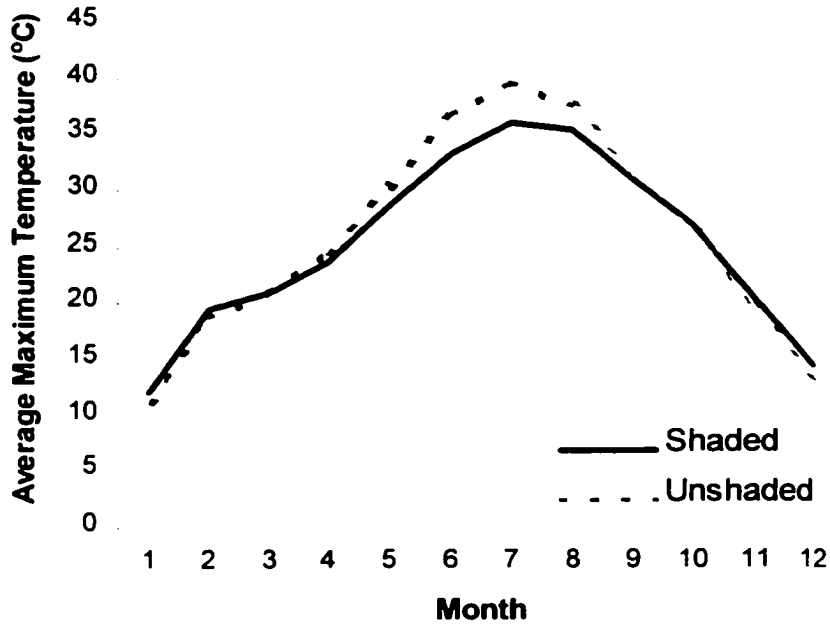

Figure 4.2. Monthly average maximum temperature for Socorro in 1995. Shaded soil surface temperature corresponds to air temperature measured, whereas unshaded soil surface temperature is more extreme (as simulated in the model).

functional groups. Subdominant desert grass species are generally shorter lived than black grama (Wright and Van Dyne 1976).

- An adjustment of aboveground turnover rates. These rates were relatively low (10 - 40 %) in the previous version of the model. However, my field experience tells me that almost all of the aboveground biomass of both grasses and forbs is turned over every year. Therefore, I adjusted the aboveground turnover rate to 77 % (allowing for perennial tissue in crowns and stems), and increased the growth rate of these functional groups to match this increase in aboveground biomass turnover.

- An adjustment of the optimum temperature for growth of C3 species to 25°C, and that of C4 species to 35°C. This adjustment was necessary as maximum temperature each day is used as the daytime temperature in the model (as opposed to average temperature). The differences in the temperature optimum between these functional groups reflects the finding that their phenological activity is separated in time, with C3 species growing mostly in spring and fall, and C4 species growing mostly during the summer (Kemp 1983).

- An increase in water use efficiency of both dominant species. The water use efficiency of black grama was adjusted to reflect greenhouse measurements, in which black grama was able to produce 1 g of biomass on as little as 394 g of water (Dwyer and DeGarmo 1970). In comparison, water use efficiency of creosotebush is relatively low. However, this species is able to control transpiration more effectively than other species and can tolerate low xylem water potential (Barbour et al. 1977). Since the model can not easily be altered to simulate such differences in the ability of species to use water, I incorporated this effect in the water use efficiency of creosotebush.

Table 4.1. Species and functional group characteristics in the model.

Species name	Maximum lifespan	Growth rate	Root turnover rate	Biomass turnover rate	Seed dispersal distance	Seed establishment probability	Water use efficiency (WUE)	Optimum temperature for growth	Fine: coarse root biomass ratio	% root biomass in 1st soil layer	% root biomass in 2nd soil layer	% root biomass in 3rd soil layer	% root biomass in 4th soil layer
B. eriopoda	40	0.7	0.25	0.67	100	0.06	22.0	35	1.3	5	50	35	10
L. tridentata	400	0.45	0.15	0.37	3	0.03	22.0	25	0.8	5	35	40	20
C3 perennial subshrubs	10	0.67	0.25	0.5	10	0.09	12.4	25	1	10	30	30	30
C4 perennial grasses	25	0.80	0.25	0.77	10	0.09	17.5	35	1	10	45	35	10
C3 perennial grasses	25	0.80	0.25	0.77	10	0.04	12.4	25	1	10	45	35	10
C4 perennial forbs	15	0.82	0.25	0.77	10	0.11	17.5	35	1	20	25	30	25
C3 perennial forbs	15	0.82	0.25	0.77	10	0.11	12.4	25	1	20	25	30	25
C4 annuals	1	0.95	1.0	1.0	100	0.25	17.5	35	1	30	50	1	10
C3 annuals	1	0.95	1.0	1.0	100	0.25	12.4	25	1	30	50	1	10

For unknown species characteristics, minor tuning of the model was necessary such that the abundance of each functional group and the dominant species corresponded, roughly, to field observations. (Rigorous testing of this was done only after simulation experiments were completed - see Verification of the model.) Germination conditions for all species were specified such that the temperature had to be at least 10°C and could not exceed 38°C (Beatley 1974). The water potential of the soil water in the first soil layer had to be no lower than 5 bars (0.5 MPa) for 4 days in order for germination to be possible (Minnick and Coffin 1999).

V. Simulation experiments

The model was run simulate a period of 130 years, thus repeating the sequence of historical weather data twice. The first 65 years were used to initialize the model. The second 65 years of the simulation were then assumed to reflect vegetation dynamics through the period of 1931 - 1995. Because of the strong climatic fluctuations during these 65 years of historical weather, only the last 20 years of the simulated results were considered for evaluation (see Analysis of results). Each experiment was run once for a 10 m x 10 m grid divided into $1m^2$ plots (100 plots). The results reported are based on 20 yearly averages of aboveground biomass of functional groups on this $100m^2$ grid. In each experiment, I evaluated the influence of the parameter(s) manipulated on subdominant functional group composition, as well as on possible explanatory variables for these changes.

Experiments manipulating the biotic structure. To evaluate the influence of biotic characteristics of the dominants on subdominant functional group composition within the model, I conducted a series of simulation experiments in which black grama

(*B. eriopoda*) was effectively transformed into creosotebush (*L. tridentata*). Black grama and creosotebush differed in eight characteristics: maximum lifespan, growth rate, biomass turnover rate, establishment probability, seed dispersal distance, optimum temperature for growth, fine root to coarse root ratio, and root distribution (Table 4.1). Starting from the species characteristics as defined for black grama, these eight parameters were changed - one at a time - to species characteristics as defined for creosotebush. Since the order of changing the parameters could influence the simulation results, I selected the order of the parameters by minimizing the change in average biomass of the dominant from one step to the next. This was repeated until all eight parameters had been changed from the values defining species characteristics of black grama to the values defining creosotebush. The successive retention of new parameters allowed me to conduct this series of experiments using 36 simulations, rather than the 256 (2^8) simulations necessary for trying all possible combinations of these parameters. This allowed me to see which species characteristics were most critical for the dominance of black grama and of creosotebush. I also used results from this experiment to evaluate how each these eight species characteristics influences subdominant functional group composition.

Experiments manipulating abiotic conditions around the dominants. I conducted two experiments, one manipulating the litter retained for black grama, and a second changing temperature in plots dominated by creosotebush. For black grama, I retained 40 % more standing dead litter for the simulation experiment. For creosotebush, I changed the temperature according to the above-mentioned function (see Modifications to the model) when creosotebush had reached a sufficient size to shade at least 30 % of a

plot of 1 m^2. Creosotebush biomass was converted to area covered using a regression equation from the literature developed for this species (Ludwig et al. 1975):

$$\text{Area} = \sqrt{\frac{\text{Biomass}}{1504}}$$

The idea that the phenological activity of creosotebush is affected by its own shade is not entirely realistic. However, this mechanism was left in the model as observations reported in the literature suggest that high temperatures do not impair the photosynthetic activity of creosotebush (Barbour et al. 1977). Because of the low temperature optimum for creosotebush growth (Table 4.1), the shading of plots on which creosotebush grows indirectly simulates the capacity of this species to grow during the hot season. The output from simulation runs incorporating changes in abiotic conditions was compared to output from simulation runs that did not include such changes (controls).

Experiments including both dominants. All of the above experiments were conducted including only one of the dominants. Since the combined effect of the dominants on subdominant functional group composition may be different from the separate effects of these dominants, I conducted a series of simulation experiments in which I included both dominants, with and without changes in abiotic conditions induced by these species. This also allowed me to evaluate how the relative abundance of these two dominants may be influenced by competition with each other as well as by their different effects on the abiotic environment.

VI. Analyses of results

Output from the model included average aboveground biomass in the 100 plots for each species or functional group. As climate is quite variable in arid regions, even

this average was very dynamic over time; it seemed, however, to vary around a constant mean for the last 20 years of the simulation. For all the simulation experiments, a one-way analysis of variance for each functional group was conducted separately to test for any significant differences between experiments during those last 20 years of the simulation (Anova Procedure, SAS Institute Inc. 1988). Differences between means were tested using a t-test (alpha = 0.05).

VII. Verification of the model

For verification of the model, the results from the simulation experiment were compared to field data from microsites around black grama and creosotebush (Chapter 2). These data were gathered at a desert grassland-shrubland transition zone at the Sevilleta LTER in September of 1997 during the peak of herbaceous growth. Subdominant species abundance in microsites around individual black grama grasses and creosotebushes was sampled using small-scale sample plots of varying size (for a detailed description of the sampling method, refer to Chapter 2). Several samples were taken from forty-five $100m^2$ areas. Subdominant functional group abundance in these microsites was summed from all microsites around black grama within each $100m^2$ area to reflect subdominant functional group abundance in a black grama dominated landscape, and from all microsites around creosotebush to reflect functional group abundance in a creosotebush dominated landscape. The percentage of the total subdominant abundance each functional group accounted for was determined. For each functional group the average of this percentage from all 100 m^2 areas was compared to the average percentage of subdominant biomass in both a simulated black grama- and a creosotebush-dominated landscape.

Results

I. Experiments manipulating the biotic structure.

When species characteristics as defined for black grama were successively changed to species characteristics of creosotebush, the smallest changes in dominant biomass were initially found with characteristics that negatively influenced dominant biomass (Figure 4.3). These characteristics included the growth rate, the fine: coarse root biomass ratio, seedling establishment probability, and seed dispersal distance. Black grama is more competitive with respect to these four characteristics than creosotebush. The difference in root distribution between the two dominants had the least influence on dominant biomass. Biomass turnover rate and lifespan were changed last to parameters characterizing creosotebush. When this was done the dominant species that now had all the characteristics of creosotebush gained back its dominance in the simulated landscape. Therefore, an important life history characteristic of creosotebush for its dominance in the landscape is the conservation of biomass over time by its long lifespan and its low yearly biomass turnover rate. In contrast, black grama dominates mainly by characteristics that help it recover from disturbance quickly, as well as its ability to explore water resource on a small scale. Both dominants have a higher water use efficiency than do subdominants (Table 4.1), a factor contribution to their dominance of the vegetation (not shown).

The influence of these changes in the characteristics of the dominants on subdominant functional group abundance depended on the parameter changed as well as on the subdominant functional group under consideration (Figure 4.3 and Table 4.2). C4 perennial grasses and forbs, as well as C3 perennial subshrubs and grasses had a higher abundance when creosotebush dominated the landscape than when black grama was the dominant (first row, Table 4.2). The abundance of annuals was completely independent of dominant species characteristics. Competition for water seems to have both direct and indirect effects on perennial subdominant functional group abundance. A direct effect can be observed in the increase of C4 perennial grass, C4 perennial forb, C3 perennial subshrub, and C3 perennial grass abundance, when root distribution, fine: coarse root biomass ratio, and growth rate were changed from values defining black grama to

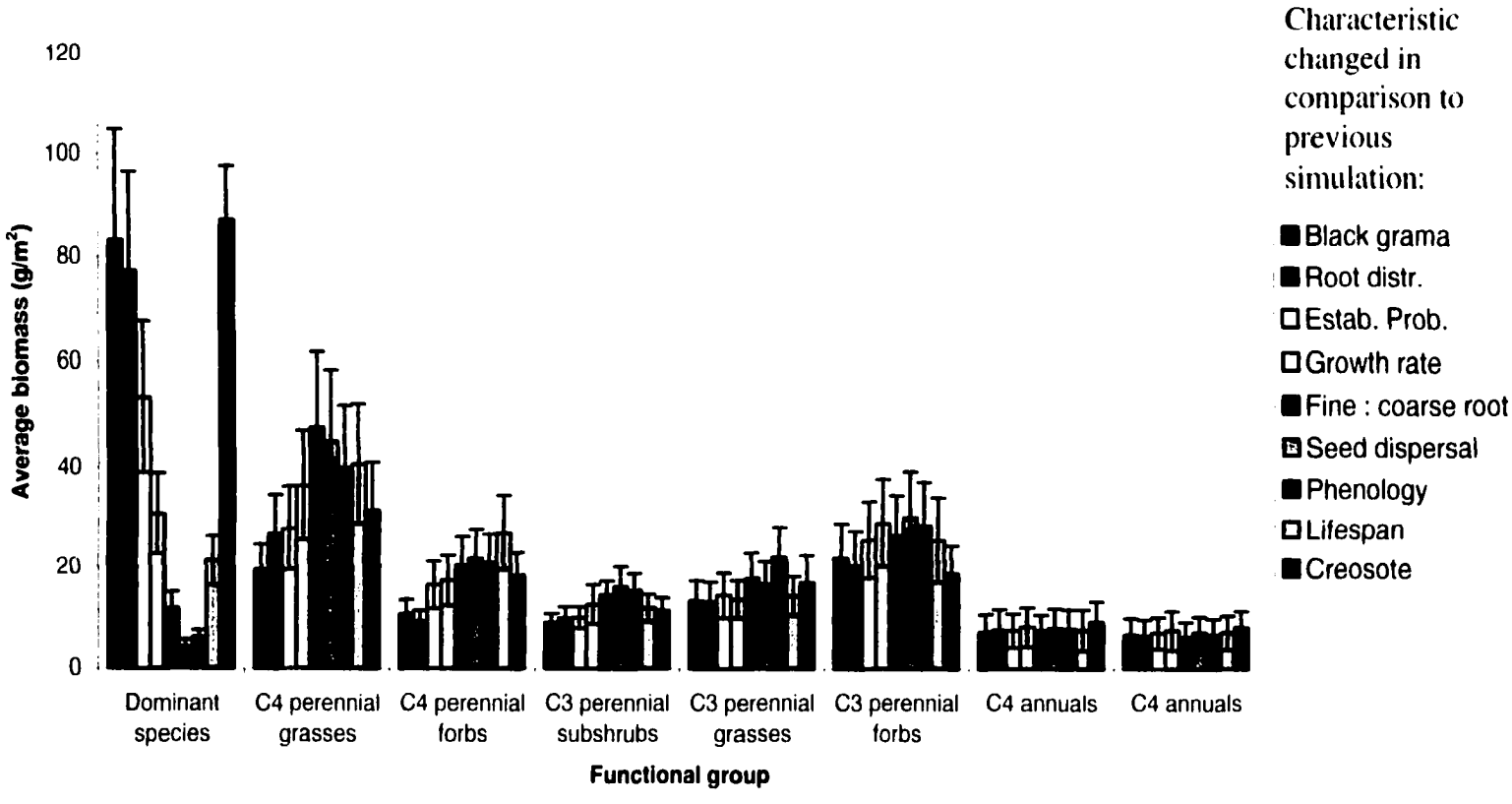

Figure 4.3. Biomass of the 'dominant species' and subdominant functional groups averaged over 20 years (error bars indicate standard deviation). The 'dominant species' was successively changed from black grama to creosotebush by changing parameters of species characteristics one by one. Each definition of the 'dominant species' incorporates one additional characteristic of creosotebush, which is indicated in the legend (see also Table 4.2).

Table 4.2. Simulated transformation of black grama characteristics into creosotebush characteristics and influence on subdominant functional group composition. (NS = non-significant result, lower = biomass of subdominant functional group significantly lower in comparison to previous simulation, higher = biomass significantly higher in comparison to previous run).

	Characteristics of dominant defined according to		Change in biomass of functional group in comparison to previous run (#) significant? (The first line compares black grama and cresosotebush (#1 and #9)) (alpha = 0.05)							
#	Black grama	Creosotebush[1]	Domi-nant (hybrid)	C4 perennial grasses	C4 perennial forbs	C3 perennial subshrub	C3 perennial grasses	C3 perennial forbs	C4 ann-uals	C3 an-nuals
1	All	None	NS	Higher	Higher	Higher	Higher	NS	NS	NS
2	All, except for*	*Root distribution (RD)	NS	Higher	NS	NS	NS	NS	NS	NS
3	All, except for*	*RD, Establishment probability (EP)	Lower	NS	Higher	NS	NS	Higher	NS	NS
4	All, except for*	*RD, EP, Growth rate (GR)	Lower	Higher	NS	Higher	NS	NS	NS	NS
5	Seed dispersal distance (SD), PH, LS, TR	RD, EP, GR, Fine:coarse root biomass ratio (FR)	Lower	Higher	Higher	Higher	Higher	NS	NS	NS
6	Phenology (PH), LS, TR	RD, EP, GR, FR, Seed dispersal distance (SD)	Higher	NS	NS	NS	NS	NS	NS	NS
7	Lifespan (LS), TR	RD, EP, GR, FR, SD, Phenology (PH)	NS	Lower	NS	NS	Higher	NS	NS	NS
8	Biomass turn-over rate (TR)	RD, EP, GR, FR, SD, PH, Lifespan (LS)	Higher	NS	Higher	Lower	Lower	NS	NS	NS
9	None	All	Higher	Lower	Lower	NS	Higher	Lower	NS	NS

[1] The last characteristic listed is the characteristic changed from one experimental simulation (#) to the next.

creosotebush values (Table 4.2). An indirect effect may be observed in the increase in C3 perennial grass abundance with an increase of the lifespan of the dominant, and a decrease in biomass turnover rate. These two changes generally had a negative influence on subdominant functional group abundance, which may have had the effect that C3 perennial grasses were released from competition with other subdominants. This indicates that in a creosotebush-dominated landscape competition among subdominant species may be just as important as competition with the dominant. C3 as well as C4 perennial forbs seemed to be sensitive to the establishment probability of the dominant, as both of these subdominant functional groups increased when the establishment probability of the dominant decreased (Table 4.2). Although the restriction in seed dispersal distance decreased the average biomass of the dominant on the landscape, it did not have any additional influence on subdominant functional group abundance.

II. Experiments manipulating abiotic conditions around the dominants.

Additional standing dead biomass did not have a significant influence on the abundance of black grama (*B. eriopoda*), nor did it have an influence on subdominant functional group abundance (Figure 4.4a). However, there was a slight trend towards higher black grama, C4 perennial forb and C4 annual forb abundance, and lower C4 perennial grass abundance. Since the difference in these results was so slight, I performed a check of the model's manipulation of litter. I found that there was consistently more litter on the plots in the simulation run with additional litter (Figure 4.4b). Evaporation, which was expected to vary in this simulation, only showed a difference in value in 5 years out of the 20 years considered (Figure 4.4c). This indicated that the model in its current version is not very sensitive to differences in litter, which maybe due to its current structure. At the end of each year the plots are classified into one of 20 'production classes' (see Methods). This information is used in SOILWAT to

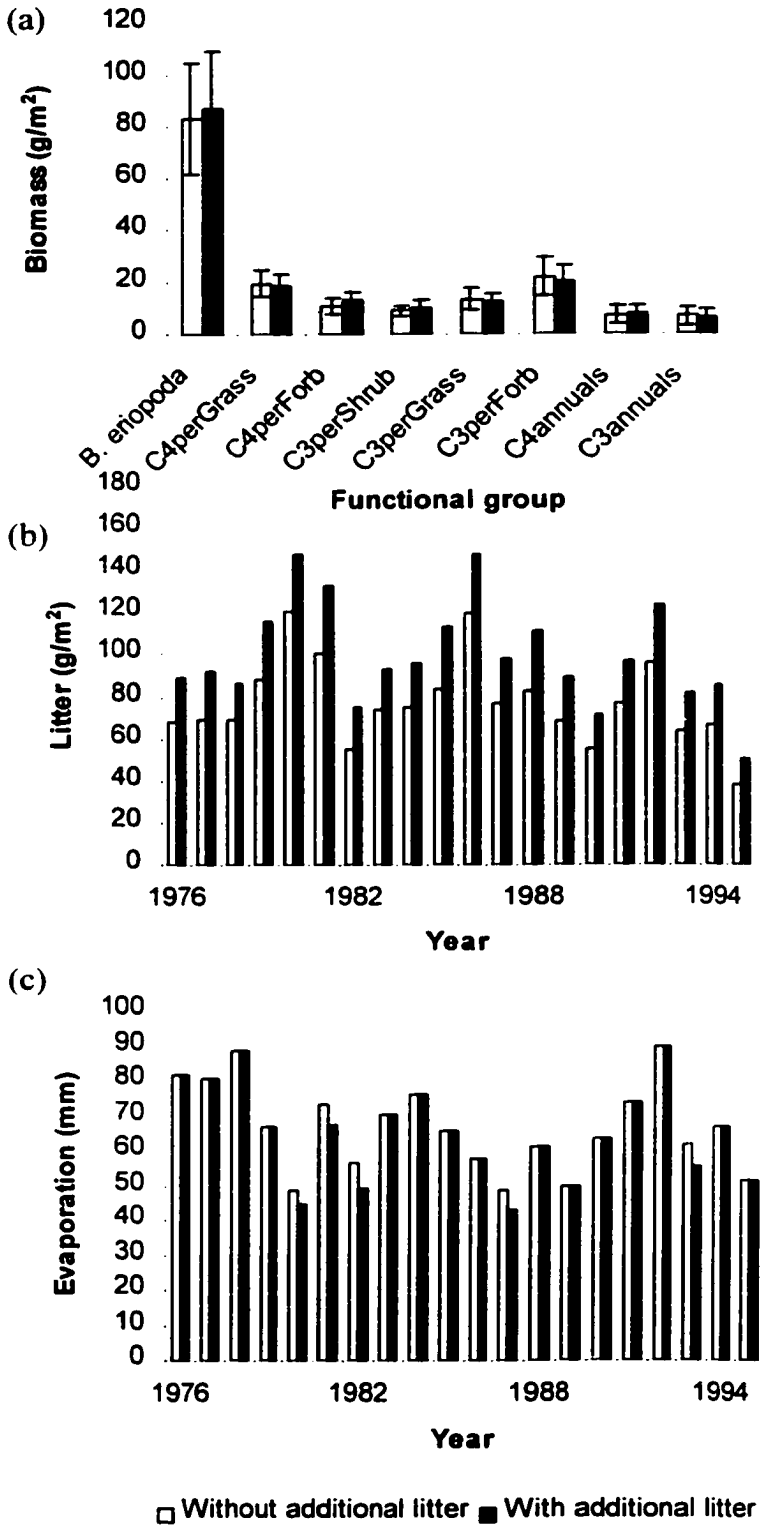

Figure 4.4. Effect of additional standing dead biomass (litter) of black grama. (a) Average biomass of functional groups over 20 years (Error bars indicate standard deviation) (b) Amount of litter per year (c) Evaporation from the soil per year.

calculate available water for plant growth and evaporation. The difference in the amount of litter in control and manipulated plots was on average less than 75 g. Thus plots were not classified into a different production class even with increased litter. As a consequence abiotic conditions on the plots were the same as those without additional litter. Adjusting the model to incorporate finer intervals in production classes would probably accentuate the trends in the results; and significant effects of the additional standing litter might then be observed. However, more production classes would have to be defined, significantly increasing the computing time necessary for the simulations, as SOILWAT has to be run for each production class.

Contrary to my expectation, the shading of creosotebush had a negative influence on average creosotebush biomass in the landscape simulated (Figure 4.5a). C4 perennial grasses and C3 perennial forbs increased with shading. It may be that these functional groups were released from competition with creosotebush, since the average biomass of the dominant was lower, and these functional groups reacted negatively to creosotebush species characteristics in the above biotic factors experiment. It is difficult to explain why the average biomass of creosotebush was lower with shading. Two processes are affected by temperature in the model: phenological activity and germination conditions. Shading extends the phenological activity of creosotebush, a C3 species, and increases its capacity to compete for available water (Figure 4.5b). Nevertheless - similar to the average biomass on the landscape - plots dominated by creosote also supported less creosote biomass with shading than in the control (not shown). This could be due to both slower growth and slower establishment of creosotebush. Slower growth in shaded plots is not very likely, since the extended phenological activity should have a positive

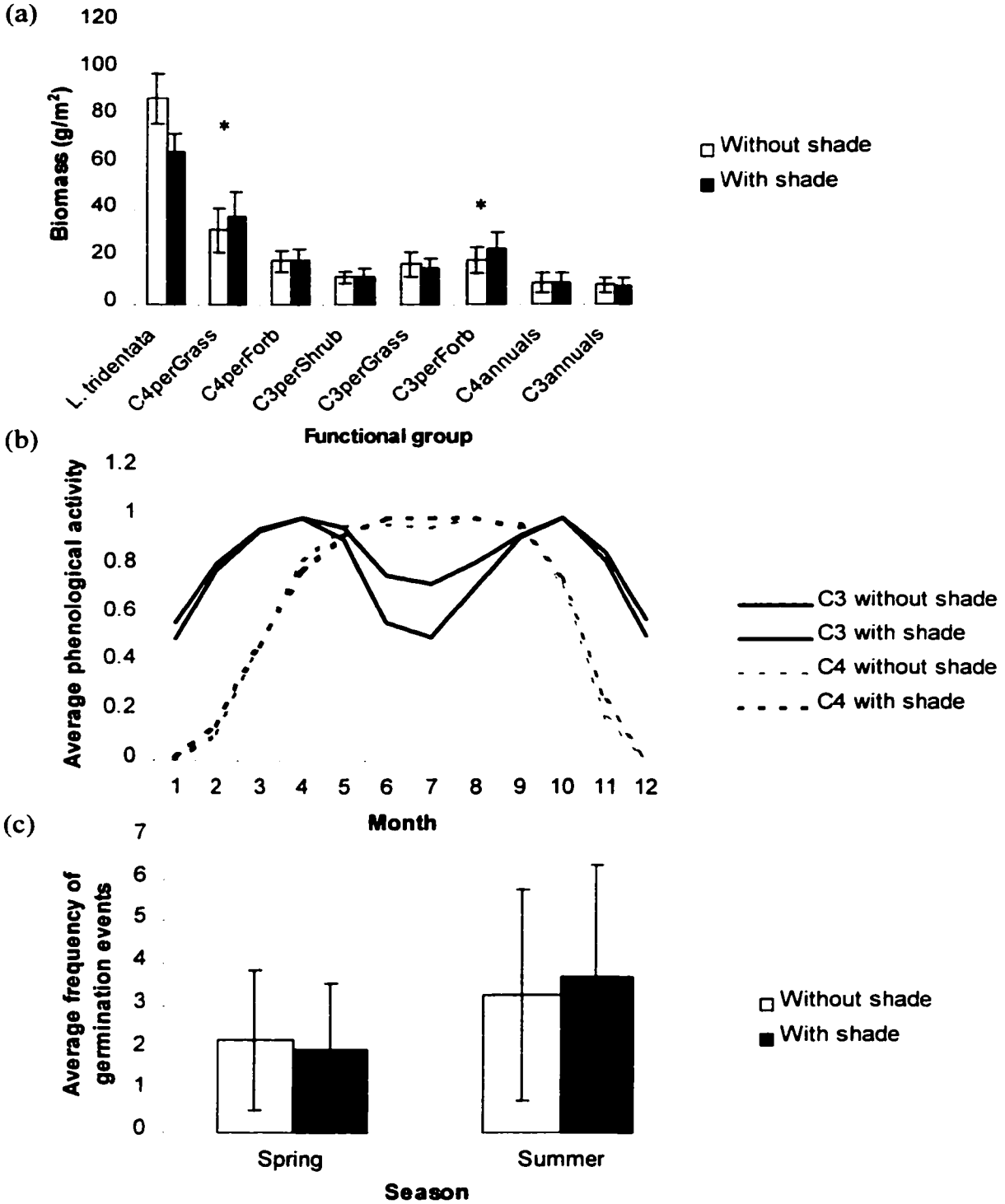

Figure 4.5. Effect of shading by creosotebush canopy. (a) Average biomass of functional groups over 20 years (error bars indicate standard deviation, stars indicate significant differences). (b) Average phenological activity/month for C3 and C4 species in shaded and unshaded plots. Creosotebush is a C3 species. (c) Frequency of germination conditions/season ('summer' includes May - August, 'spring' includes rest of the year (both spring and fall)).

influence. It could have been the case that creosotebush generally established later in the simulation run and therefore could not grow to the same size as in the control run. To test this I checked the number of days occurring in each season when the specified germination requirements were fulfilled (see Methods). However, there were no significant differences between the number of germination days in the spring and the summer with and without shading (Figure 4.5c). Furthermore, variation in establishment of creosotebush in plots dominated by this species should not have a strong influence on the average dominance in the simulated landscape, since plots shaded are already dominated by this species. Therefore, neither of the two mechanisms affected directly by temperature can explain the decrease in dominant biomass. It may be that indirect effects - particularly competition with C3 perennial subshrubs and grasses - influenced these results.

III. Experiments including both dominants.

Generally, the subdominant functional group abundance in simulations with both dominants was similar to the subdominant functional group abundance in vegetation dominated by black grama (Figure 4.6a). The only exception was the abundance of C3 perennial grasses and forbs, which was significantly lower when both dominant species were present. When changes in abiotic conditions around dominants were added to the model, only C4 perennial grasses exhibited changes in their average biomass (Figure 4.6b). In contrast to the simulation with black grama as the only dominant, additional litter had a significant negative influence on C4 perennial grass abundance when both dominants were present. I checked if litter manipulation was more successful when two dominants were present, but found that evaporation was still similar to evaporation in the

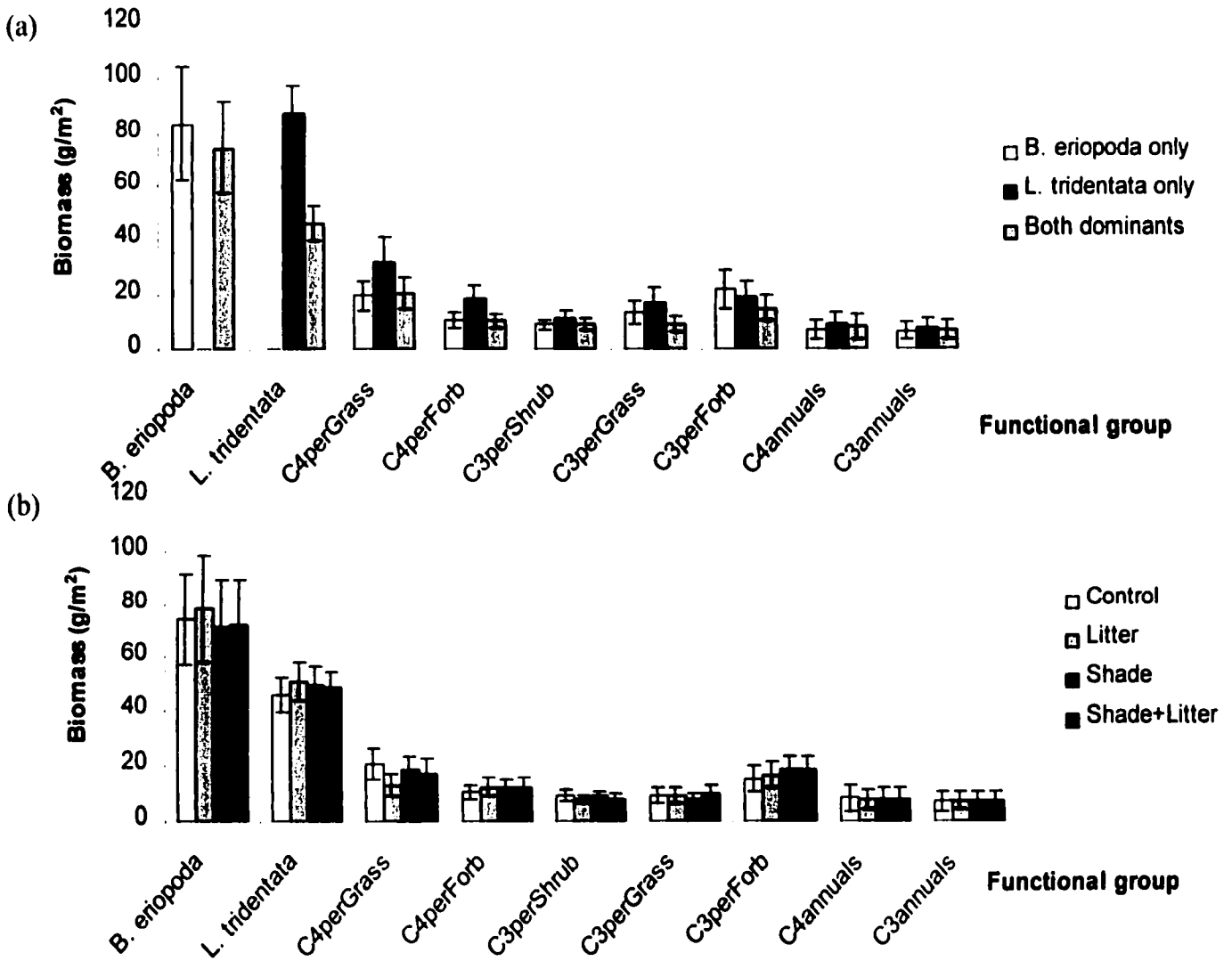

Figure 4.6. Average biomass of functional groups over 20 years (error bars indicate standard deviation). (a) Comparison of landscapes dominated by either black grama (*B. eriopoda*) or creosotebush (*L. tridentata*) or both species. (b) Comparison of landscapes dominated by both species with and without feedback loops to influencing abiotic conditions around the dominants.

control (without additional litter). Therefore, this decrease in C4 perennial grass abundance can only be explained indirectly by the increase in creosotebush biomass in the presence of litter. When shade alone, or shade and litter were manipulated, subdominant species abundance did not change significantly.

IV. Verification of the model.

The observed relative abundance of subdominant functional groups corresponded fairly well to the simulated relative biomass of these groups, except for higher relative biomass of C3 perennial grasses in the simulations (Figure 4.7a). This functional group is extremely rare at the Sevilleta and the mechanism that contributes to its rarity was not captured in the model. It may be that this functional group is restricted by seed availability in the regional species pool, or that C4 perennial grasses have more extensive vegetation periods than simulated in the model and thus can outcompete C3 perennial grasses. Some of the differences between the observed and simulated data may stem from the difference in the variables measured (abundance vs. biomass) and the differences in the time span of the observation (one season - one year observation vs. whole year - 20 year simulation). In particular, the differences in the abundance of annuals may be explained by observation timespan.

Comparison of these results with the simulations addressing possible changes in abiotic conditions (Figure 4.7b) shows that the difference in the C4 perennial grass abundance between creosotebush- and black grama-dominated landscapes are enhanced when these processes are included; this result corresponds more closely to the observed data. However, for all the other functional groups feedback loops increased the disparity between the observed and simulated data. This suggests that even though general trends

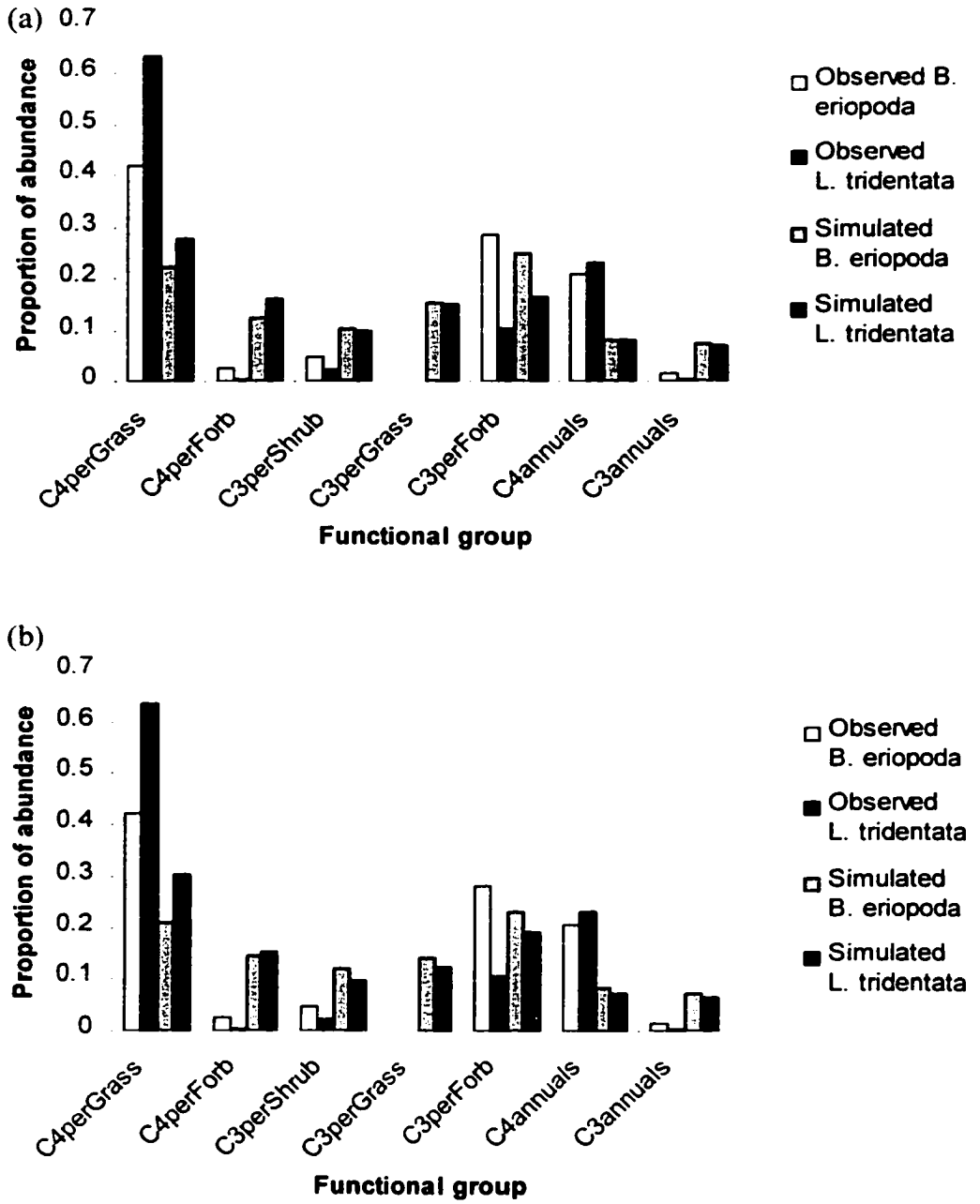

Figure 4.7. Comparison of observed versus simulated relative abundance of subdominant functional groups in black grama (*B. eriopoda*) and creosotebush (*L. tridentata*) dominated landscapes. (a) Comparison with simulated biomass in simulations incorporating only biotic differences between dominants. (b) Comparison with simulated biomass in simulations incorporating additional litter with black grama and shade with creosotebush.

in subdominant functional group composition could be simulated using this model, not all the mechanisms determining subdominant functional group abundance at this grassland-shrubland transition zone were incorporated into the model. Long-term field data on biotic and abiotic processes in desert grasslands would help to identify such mechanisms and better parameterize the model.

Discussion

The mechanisms involved in plant species coexistence patterns have been explored in previous studies (Phillips and MacMahon 1981, Czárán and Bartha 1989, Bartha et al. 1995, Kobe 1996, Peters submitted). These studies identified competition, establishment, phenology and mortality as important mechanisms governing species coexistence patterns. In this study, I used these mechanisms to investigate how two dominant species, which can replace each other over time, influence subdominant functional group composition at a desert grassland-shrubland transition zone. I also explored how effects of the dominants on abiotic conditions affected species coexistence patterns. In my discussion, I consider three things: first, the simulation model used for this study; second, the biotic characteristics of the dominant species shown to influence subdominant functional group composition; and third, abiotic feedback loops.

I. Discussion of the model

The model used was a model of intermediate complexity compared with other ecological models (e.g. Czárán and Bartha 1989, Pacala et al. 1996, Parton et al. 1998). Resource distribution was modelled explicitly, albeit not mechanistically, and plant processes were simulated phenomenologically, rather than based on detailed plant physiological processes. However, plant functional types and species were defined in

more detail concerning their life history, phenological, physiological and structural characteristics than is the case in simple plant models (Czárán and Bartha 1989, Smith and Huston 1989). Overall, it appears that the model may gain precision by incorporating more mechanistic processes. But such improvements have to be carefully weighed by the level of detail that is useful when attempting to simulate landscape scale vegetation patterns. Furthermore, controls on plant processes may change with scale (Jarvis and McNaughton 1986), and often a mechanistic understanding of processes at large scales is lacking (Roberts and Gilliam 1995). A promising approach is to hierarchically structure the model (Luxmoore et al. 1991, R. H. Gardner, pers. comm.). In this approach, small-scale mechanistic models are used to estimate certain key parameters for the part of the model addressing large-scale phenomena. The classification of the plots into production classes in the current model is an attempt to implement such a structure in this model, but further refinement is necessary. Such a development of the model would parallel attempts to include more mechanistic details in forest gap dynamics models (Urban and Shugart 1992, Pacala et al. 1996).

Characteristics of plant functional groups as used in the model were sensitive to the mechanisms investigated and their relative abundance was simulated with fair accuracy. Successful use of this model to simulate relative functional group abundance was also made in previous studies (Humphries et al. 1996, Peters submitted). However, the definition of functional groups could be further refined using, for example, a classification system that includes a distinction between shallow and deep root species within each functional group, or carbon allocation patterns of species (e.g. Golluscio and Sala 1993, Coffin and Lauenroth 1996, Kobe 1997). However, within functional groups

the range of species' adaptations is wider than their classification into the same functional group would suggest (Smith 1997, Walker et al. 1999). Even a refined classification of species into functional groups can not fully capture the variety of ecological adaptations of plant species to their environment, and a certain degree of simplification will always be required to be able to simulate ecosystem dynamics at large scales (Körner 1993). The most useful classification will be one in which species are grouped with respect to characteristics that most likely will influence the processes of interest. The model in its current version is sensitive enough to explore changes in the vegetation that may occur due to different management regimes; coupled with geographic databases, it could be used to evaluate management decisions (Peters and Herrick 2001). However, if processes of vegetation - atmosphere, or vegetation-soil feedback loops are of interest further refinement of the model may be necessary.

II. Differences in biotic characteristics of the dominants

Black grama dominance can be simulated satisfactorily in this model, as has been found in a previous study (Peters submitted). However, some important species characteristics of creosotebush, such as its widespread root system and its possible allelopathy (Gile et al. 1998, Schenk et al. 1999), can still not be simulated with this model. Further work to enhance water flow between plots is needed to be able to simulate an extended root system. A submodel simulating allelopathy has been developed for this model, although it was not used in the current version (S. Goslee, pers. comm.). Nevertheless, some fundamental differences between creosotebush and black grama could be simulated based on the characteristics incorporated. Whereas black grama dominates the vegetation by its competitive ability and its capacity to re-establish

after disturbance, creosotebush seems to acquire dominance by 'persistence'. This corresponds well to literature reports of the ecological strategies of these two dominant species (Barbour et al. 1977, Gosz and Gosz 1996).

Rather than presenting a threat to the diversity of functional groups of grasslands, I found that subdominant functional group abundance in shrub dominated landscapes was higher than in grass dominated ones. This corresponds to observations that diversity around shrubs is high, at least during initial stages of shrub encroachment (Chapters 2 and 3). The effect of the different biotic characteristics of the dominants depended on functional groups, as well as indirect effects that altered competitive relationships among subdominant functional groups. Plants often occur in environmental conditions at the edge of the range of conditions they can tolerate and are displaced from places with optimal conditions by competitively superior species (Smith and Huston 1989). A slight alteration of the competitive relationships in the plant community, induced by changes in the life history and competitive capacity of the dominant species, can therefore alter species coexistence patterns, as shown in this study. However, as for other simulation models, few field observations are available to test these results (Urban and Shugart 1992). The comparison made in this study suggests that for some functional groups additional mechanisms not built into the model may be responsible for the pattern observed. Field observations on the phenology, dynamics of root distribution and water uptake, as well as the competitive relationships between species would help to improve the model. In particular, the dynamics of annuals are not simulated the best they could be; phenological clues of annuals are not well understood in arid ecosystems (Bowers

1987). A combined effort of simulation modelling and field experiments is necessary to improve our understanding of vegetation dynamics (Peters submitted).

III. Abiotic changes around the dominants

The changes in abiotic conditions around dominant plants - especially shrubs and trees -have been studied previously, but few attempts have been made to link these changes to subdominant species composition (Olsvig-Whittaker 1988, Specht and Specht 1989). Feedback loops between plants and environmental conditions are especially important in extreme environments under conditions stressful for plant life (Callaway and Walker 1997, Hacker and Gaines 1997). The results from this study indicate that feedback loops between the dominant plants and the abiotic environment could be potentially important in determining relative dominant and subdominant abundance. Field studies of abiotic conditions and their influence on the occurrence of dominant plants are needed to increase our understanding of these feedback loops and the accuracy of the first attempts to build such feedback loops into the model. Apart from plant-soil feedback loops concerning temperature and water dynamics, feedback loops involving different resources for plant life, such as light and nutrients, should also be taken into account. This is especially important as the two dominant species studied here have been found to have different effects on nutrient dynamics (Kieft et al. 1998, Gill and Burke 1999).

The feedback loops as implemented in this model suggest that shading by creosotebush induces a negative feedback loop reducing creosote dominance over time. In contrast, tendencies seen in the results of increased litter in black grama dominated plots seem to indicate that this mechanism may induce a positive feedback loop, thus

enhancing black grama dominance. Litter build-up in black grama canopies may also change the fire regime of desert grasslands, and thus indirectly enhance the dominance of this species with respect to woody species which may loose seedlings during fire (McPherson 1995). The contrast in the effect of the abiotic feedback loops on these dominants further emphasizes the finding from this study that creosotebush would take a very long time (hundreds of years) to outcompete black grama in the absence of disturbance factors which reduce the vigor of black grama populations. Rapid changes of dominance as reported in the literature are therefore most likely due to factors not simulated in this study, such as grazing by domestic livestock and climatic changes (Grover and Musick 1990, Van Auken 2000). In the absence of grazing, shrub encroachment under current climatic conditions is a very slow process. In the event of expected climatic changes, the directionality of this process may easily be changed before black grama is outcompeted in areas it currently occupies (Peters submitted). Only land use that significantly impacts grass cover will induce the desertification process observed in many semi-arid and arid landscapes around the world (Darkoh 1998, Fredrickson et al. 1998, Van Auken 2000). Therefore, future simulation modelling of vegetation changes in the Southwestern United States may also have to include components addressing social and economic dynamics.

Summary

A gap dynamics model (ECOTONE) was used to explore the implications of differences in biotic characteristics of two dominant species for subdominant functional group composition. Two mechanisms inducing abiotic feedback loops around these two dominant species were also investigated. I found that the importance of differences in

biotic characteristics of the dominants depended on the subdominant functional group, with perennial forbs being more sensitive to characteristics influencing establishment, and perennial grasses more sensitive to characteristics influencing competition for water. Annuals were not sensitive to the change in the dominant species. The abiotic feedback loops simulated suggest that interactions of the dominant species with their environment may have a positive influence on black grama and a negative influence on creosotebush. The influence of biotic and abiotic factors on subdominant functional group composition was difficult to predict not only because competitive relationships between the dominants and the subdominants were altered, but also because of competitive relationships among subdominant functional groups. Comparison with field data suggests that further refinement of this model is required in order to more accurately simulate vegetation dynamics and feedback loops involving the abiotic environment.

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V. SUMMARY AND CONCLUSIONS

Understanding species diversity patterns has long been a concern in plant ecology (Juhász-Nagy 1984, van der Maarel 1996). With the increasing awareness of the importance of biodiversity to ecosystem functioning, understanding the mechanisms that create and maintain species diversity has become crucial for the development of appropriate conservation measures (Tilman 1996, Chapin et al. 1997, Walker et al. 1999). Species loss from ecosystems can be due to many factors, but in arid ecosystems it is often linked to a general degradation of the ecosystem, called desertification (Huenneke and Nobel 1996). In many areas of the world, desertification is associated with a shift in the dominant lifeform from grasses to shrubs (Van Auken 2000). In this dissertation I investigated if and how a shift in dominance from black grama (*Bouteloua eriopoda* [Torr.] Torr.) to creosotebush (*Larrea tridentata* [Sessé & Moc. ex DC.] Coville) in desert grasslands, could be causally connected to species loss. I used spatial pattern analysis and simulation modelling to address these questions.

Contrary to previous studies that documented low species diversity in creosotebush dominated areas (e.g., Peters 2000, Whitford et al. 2001), I found in all three parts of this study that in a ecotone situation the shift in the dominant lifeform was not associated with species loss. The encroachment of grassland by shrubs increased the spatial heterogeneity of the vegetation at the ecotone investigated, and as a consequence, plant species diversity also increased. Part of the discrepancy between the results from this study and the studies mentioned above, may have originated from differences

between the study areas. My study was conducted at an ecotone. Ecotones often have a higher diversity than adjacent vegetation types because of the mixing of floras in the transitional zone between vegetation types (Neilson 1993). The studies mentioned above found low diversity in core areas of *L. tridentata* dominance. Furthermore, processes associated with desertification, such as soil erosion and overgrazing that occur concurrently with shrub encroachment, were not taken into consideration in my study. Field observations were made in a relatively recently encroached area that has been protected from grazing since 1973 and some indirect processes that maybe induced by *L. tridentata* where it dominates larger areas (e.g., Schlesinger et al. 1990), may not have the same importance in an ecotone situation. Further research on these indirect effects of *L. tridentata*, and their importance in *L. tridentata* dominated areas of varying extent is needed to increase our understanding of the differences in species diversity observed in this ecotonal situation and the core areas of *L. tridentata* dominance.

This research also illustrated that differences in species characteristics, particularly morphological differences between *B. eriopoda* and *L. tridentata* were important in determining species coexistence patterns at this desert grassland-shrubland transition (Chapter 2). The importance of the morphology of dominant plants for coexistence patterns has been recognized previously (Mahdi and Law 1987). Field observations of the small-scale coexistence pattern around dominant grasses and shrubs revealed that functional groups have a different distribution in microsites around these plants (Chapter 2). Annuals tended to occur in the interspace, whereas perennials showed no clear differences in their abundance between interspace and plant canopies. These differences in the distribution of subdominant functional groups may, in part, be

explained by the phenology of these functional groups, as C3 species tended to occur underneath the shrub canopy, whereas C4 species prefer the interspace. Perennials were represented by species that had both photosynthetic pathways, whereas annuals were mostly C4 species. This corresponds to observations of the distribution of C3 and C4 species in piñyon-juniper woodlands (Breshears et al. 1998).

Investigation of species richness across scales (from the plant - scale to the transition zone - scale) (Chapter 3) revealed that disturbance is an important factor influencing annual plant species richness, whereas perennials seemed to be more responsive to heterogeneity associated with dominant plants. Kangaroo rat mounds are particularly important to maintain annual plant species richness in desert grasslands (Guo 1996). The different sensitivities of perennials and annuals to the distribution of dominants and disturbances may be explained by differences regarding the mechanisms by which dominant plants and disturbances influence species coexistence patterns. Perennials may be more adapted to competition with perennial dominant species, whereas annuals seem to cope better with disturbances that require high mobility. Management for maintaining the species richness of desert grasslands should take into account the different sensitivities of these functional groups.

Black grama (*B. eriopoda*) used different characteristics to dominate the desert vegetation than creosotebush (*L. tridentata*) (Chapter 4). Black grama was locally very competitive while creosotebush was able to conserve more resources, due to its long lifespan and low biomass turnover rate. This suggests that competition with these dominant species is different, and therefore may be associated with a shift in subdominant species composition. However, none of my studies revealed a pronounced

shift in species composition. This could be partially due to the lack of information about specific species characteristics of subdominants. Only functional groups of species could effectively be compared. Alternatively, factors not investigated in this study create sufficient heterogeneity around these dominants so that microhabitats exist for all species around both grasses and shrubs.

Because of the nature of scientific investigations, insights gained from studies become hypotheses to be confirmed by future research and consensus in the scientific community (Pickett et al. 1994). The original methods used in this research lead to some new observations concerning the influence of dominant grasses and shrubs on ecosystem structure and function. However, even though distinguishing microsites around dominant plants was very successful in explaining species coexistence patterns at small-scales, differences between microsites have not yet been implemented in the simulation model. Furthermore, larger scale processes that require simulation of landscapes (larger than 100 m^2) can not yet be simulated. Therefore, only partial aspects of vegetation dynamics have been understood. The integration of this scientific investigation into a theory that could predict future vegetation change has not yet been achieved. However, as our knowledge of the ecological processes that influence vegetation dynamics in desert grasslands and shrublands increases, our ability to manage shrub encroached areas that are unlikely to revert to grasslands under current climatic conditions will increase, too. If future research is developed in accordance with the needs of local communities, and directed towards using the resources currently available in dryland ecosystems, scientists can still make an important contribution to coping with land degradation in these ecosystems (Fredrickson et al. 1998).

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