Assessing Plant Community Structure in the Upper Las Vegas Wash Conservation Transfer Area, Nevada: The Influence of Biotic and Abiotic Variables

Amy A. Croft
Utah State University

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ASSESSING PLANT COMMUNITY STRUCTURE IN THE UPPER LAS VEGAS WASH CONSERVATION TRANSFER AREA, NEVADA: THE INFLUENCE OF BIOTIC AND ABIOTIC VARIABLES

by

Amy A. Croft

A dissertation submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

James A. MacMahon
Major Professor

Janis L. Boettinger
Committee Member

Thomas C. Edwards, Jr.
Committee Member

Ethan P. White
Committee Member

Eugene W. Schupp
Committee Member

Mark R. McLellan
Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2016
ABSTRACT

Assessing Plant Community Structure in the Upper Las Vegas Wash Conservation Transfer Area, Nevada: The Influence of Biotic and Abiotic Variables

by

Amy A. Croft, Doctor of Philosophy

Utah State University, 2016

Major Professor: James A. MacMahon
Department: Biology

Ecological communities are complex, the structure of which is composed of interactions between multiple community characteristics and the abiotic and biotic factors shaping them. Because of this complexity, ecological studies are generally limited in scope and size, often dissecting communities into their component parts to examine them piece by piece. While this might be the most practical method to study communities, this approach often neglects other characteristics that, with their inclusion, would provide a more complete picture of community ecology. The studies described in this dissertation were conducted in an effort to synthesize the complexity that is inherent in ecological plant communities growing on a Mojave Desert bajada. Each study addresses a separate component of community structure, which, taken as a whole, provides a more thorough understanding of arid plant community dynamics. Overall, our results reveal the importance of substrate variables and their role in shaping plant community structure in arid environments. In addition, these investigations provide evidence of the strong role
that facilitation plays on this bajada and possibly arid plant communities as a whole. The comprehensive approach described in this dissertation will enable ecologists to gain a more complete understanding of community dynamics and apply this knowledge to various climate change and land management scenarios.

(236 pages)
PUBLIC ABSTRACT

Assessing Plant Community Structure in the Upper Las Vegas Wash Conservation Transfer Area, Nevada: The Influence of Biotic and Abiotic Variables

by

Amy A. Croft

By nature, ecological communities are complex. Communities are often composed of many different interacting species which, together, are influenced by the environment. Ecologists tend to study communities by breaking them into smaller parts and studying them piece by piece. While this might be the most practical method to study communities, this approach doesn’t provide a complete working picture of the entire community. The purpose of this dissertation was to investigate multiple working parts of plant communities growing in a portion of the Mojave Desert and integrate the studies for a greater understanding of how the communities function as a whole. Overall, our results show that soil properties have a strong influence on the amount of water that is available for plants to grow. This, in turn, has a large effect on plant size, how many plant species are present in one area, and how the plants are arranged on the landscape. Having a greater understanding of ecological communities as a whole will help scientists and land managers make appropriate decisions in the face of rapid urbanization and climate change.
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This research was supported by the USDA Bureau of Land Management and the USU Ecology Center. Special thanks to Gayle Marrs-Smith at the Las Vegas Field Office for field assistance. I would like to extend special thanks to the many people who helped collect field data for this project, especially my fellow students, Dr. Lori Spears, Jesse Walker, and Dr. Mary Pendergast and members of the Boettinger and Edwards labs. Statistical direction was provided by Susan Durham and Drs. Jari Oksanen, David Roberts, Ethan White, and Andrew Rayburn. I would also like to recognize the USU Ecology Center and Biology Department for financial support.

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Last but not least, many thanks to my husband, Scott Croft. Scott was exceptionally patient while I found my way through this project. I am deeply grateful for his continued love and support. My son, Benjamin Croft, provided constant light and encouragement. I hope this dissertation serves as a reminder that it takes hard work and dedication to reach your goals.

Amy A. Croft
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CHAPTER 1
INTRODUCTION

Ecological communities are inherently complex. The complexity arises from the interplay between the considerable array of characteristics that describe community structure and the various processes influencing these characteristics. MacMahon et al. (1981) describe community structure as the patterning of characteristics of the resident organisms. Community characteristics may include but are not limited to species composition, abundance, diversity, and size. Ecologists search for patterns in these characteristics in an effort to gain insights into what processes create and maintain the observed patterns (Cody and Diamond 1975, Harvey et al. 1983, Gotelli and Graves 1996, McGarigal et al. 2000, Stoll and Bergius 2005). Processes driving community structure may be generally described as abiotic pressures, biotic interactions, and historical events (Maurer 1987, Legendre and Legendre 1998).

Ecologists have long sought the relative roles of abiotic vs. biotic factors in driving community structure. Discerning the relative role of community driving processes on multiple aspects of community structure is difficult at best. Community structure is often shaped by multiple interacting processes all of which operate and interact at various spatial and temporal scales. Because of the complexity and multitude of interacting characteristics and processes, ecological studies are generally limited in scope and size, often dissecting communities into component parts to examine them piece by piece. Although valuable, this approach limits our understanding of communities as a whole.
Community ecology is in need of studies and methods that will unify and condense the various pieces to this complex puzzle.

Plant communities are ideal to study multiple aspects of community structure concurrently. Because plants are sessile organisms and share requirements for basic resources, it is more manageable to track and observe multiple patterns in community characteristics than for more multifaceted and mobile organisms. In particular, arid plant communities are considered to have a more coherent organization than more complex communities because they are relatively sparse and have fewer component populations (Chew and Chew 1965). The simplicity of plant communities in arid environments provide an opportunity to study multiple aspects of community structure concurrently in order to gain a more complete understanding of which processes regulate patterns in community characteristics.

The distribution, abundance, and size of arid plant communities are strongly influenced by both abiotic and biotic processes (Miriti 2007) and studies investigating how abiotic and biotic factors influence the structure of arid plant communities are numerous. Given that water is considered the primary limiting resource in desert ecosystems (Noy-Meir 1973, MacMahon and Schimpf 1981, Walker et al. 2001, Titus et al. 2002), water availability is usually considered as the principal abiotic driving factor for arid plant communities. As such, many studies focus on water limitation and its role in shaping plant community structure.

Drought induced perennial plant mortality may be one of the most important processes affecting plant community structure in deserts and drought response tends to be soil specific (Hamerlynck and McAuliffe 2008, McAuliffe and Hamerlynck 2010).
There have been a host of studies in the desert southwest which have investigated the role of soil properties on plant available water. The phenomenon of soil particle sorting on bajada gradients and its influence on plant communities has been well studied (Philips and MacMahon 1978, MacMahon and Schimpf 1981, MacMahon and Wagner 1985, Bowers and Lowe 1986). Furthermore, several others have compared plant water relations and growth patterns between different soil types (McAuliffe 1994, Smith et al. 1995, Hamerlynck et al. 2000, Hamerlynck et al. 2002, McAuliffe et al. 2007). Findings show that soil texture, age, and horizon development dictate water availability. Subtle differences in soil properties may lead to large differences in the amount of water that can be stored and absorbed (Yang and Lowe 1956, MacMahon and Wagner 1985, Hamerlynck et al. 2000, Hamerlynck et al. 2002, Hamerlynck et al. 2004, McAuliffe et al. 2007, Ignace and Huxman 2009, Webb 2009, Schwinning et al. 2011). Soil hydrologic properties thus direct the distribution and pattern of plant communities.


Several studies have examined how facilitation and competition are influenced by plant size and lifestage (Callaway and Walker 1997, Miriti 2006). Plant size dictates the quantity of water, nutrients, and space an individual requires for growth and survival. Some have proposed that plant-plant interactions change from facilitative to competitive as a plant grows larger (Philips and MacMahon 1981, Cody 1986, Skarpe 1991, Haase et al. 1996). Seedlings are often found spatially aggregated with adult nurse plants which improve the harshness of the environment (McAuliffe 1984, McAuliffe 1988, Callaway and Walker 1997, Toft and Fraizer 2003, Miriti 2006, Kéfi et al 2008). However, as the seedlings grow, they often become competitors of the nurse plant (McAuliffe 1988, Callaway and Walker 1997).

Of growing interest is the role of self-thinning in arid plant communities. The self-thinning rule predicts that total plant abundance per unit area should decline with increasing plant size (Enquist et al. 1998, Belgrano et al. 2002, White et al. 2007). The thinning rule is based on the assumption that plants compete for limited resources within a given area and resource supply limits community carrying capacity (Enquist et al. 1998, White et al. 2007, Ernest et al. 2009). Several studies investigating the self-thinning rule in arid environments have shown that the thinning relationship is weaker under increased aridity (Deng et al. 2006, Chu et al. 2008, Lin et al. 2013) and have proposed that facilitative interactions may offset the negative effects of competition (Deng et al. 2006,
Chu et al. 2008, 2009, 2010). Deng et al. (2006) proposed a positive relationship between plant size and abundance where facilitation is commonly observed.

Despite years of discussion and countless studies exploring the influence of abiotic and biotic variables in structuring arid plant communities, the relative contribution of these variables is still not apparent. To date, most of this research has considered the roles of abiotic and biotic processes separately, and limited their analyses to a single species or pairwise interactions. While this piecemeal approach is useful for gathering information, we are left without a clear representation of actual community dynamics. There is a need to explore the roles of both abiotic and biotic variables on multiple characteristics of interacting plant communities. A more comprehensive study plan would address the effect of abiotic factors on community abundance and diversity as well as plant-plant interactions. It would also address the role of substrate on plant size and how differences in size might influence plant-plant interactions.

The objective of this dissertation was to examine the roles of both abiotic and biotic processes in shaping multiple aspects of community structure on a Mojave Desert bajada. In 2006, a multidisciplinary team from Utah State University was tasked with creating soil and vegetation maps for a 7,400 hectare parcel of the Mojave Desert, referred to as the Upper Las Vegas Wash Conservation Area (ULVWCTA). The team used 240 vegetation sampling plots, soil survey data produced by the US Department of Agriculture Natural Resources Conservation Service (USDA NRCS), 45 soil pedons, high-resolution aerial photography, a digital terrain model, spectral imagery, and United States Geological Survey (USGS) maps (1:100,000 Geologic and Geophysical maps of the Las Vegas 30’ X 60’ Quadrangle, Clark and Nye Counties, Nevada, and Inyo County,
California (Page et al. 2005), to create detailed soil and vegetation maps for the area (MacMahon et al. 2008). This effort identified seven vegetation communities, eight soil map units, and seven geologic units and provided a large and detailed data set ideal for looking at communities as a whole.

Tilman (1982) described the characteristics of plant community structure as species composition, abundance, diversity, the spatial and temporal patterning of species abundances, and morphological characteristics of the dominant species. Collectively, this dissertation will examine the impacts that both abiotic and biotic variables have on each of these characteristics for the plant communities on the ULVWCTA. Each chapter will address different variables which together will provide a more holistic view of community structure.

Chapter 2 examines the abiotic influences on each plant community on the ULVWCTA. Research has established the strong role that abiotic properties play in structuring arid plant populations, however there is still a disconnect as to the importance of soil in addition to other abiotic variables such as geologic substrate, topography, and bioclimatic variables and their effect on extensive, conjoining plant communities. Specifically, climatic, geologic, and soil variables were evaluated for their impact on plant community abundance and distribution. Chapter 3 investigates the biotic influences within each plant community on the ULVWCTA, with special focus given to the roles of soil and geology and their impact on plant-plant interactions. Dispersion patterns were analyzed for evidence of competition or facilitation. We are aware of only one study that incorporated the influence of soil type on dispersion patterns. Schenk et al. (2003) examined the spatial pattern of a single species, *Ambrosia dumosa*, on two different
geologic substrates. Chapter 4 examines patterns in plant size and abundance across the ULVWCTA and also gives attention to the influence of soil and geology in shaping plant size and abundance patterns. We also investigate the self-thinning relationship and its applicability in this arid environment. We are aware of only two studies that have reported a negative relationship between *Larrea tridentata* density and average plant size (Chew and Chew 1965, Allen et al. 2008), neither of which took an entire community into consideration. Chapter 5 provides a discussion and general conclusions of these studies. This dissertation attempts to bridge the gaps between discrete subjects in community ecology, taking into account multiple community characteristics and the abiotic and biotic processes shaping community structure.

LITERATURE CITED


CHAPTER 2

ABIOTIC INFLUENCES AND PLANT COMMUNITIES ON A MOJAVE DESERT BAJADA: A MULTIVARIATE ANALYSIS

Abstract. Although it is known that soil, geology, topography, and bioclimatic factors influence the structure of arid plant communities, the relative contribution of these factors remains unclear. In order to disentangle the role of these abiotic variables, this study used two fundamentally different multivariate ordination techniques to examine patterns in species composition and abundance on a Mojave Desert bajada. The patterns revealed were consistent with our predictions that woody perennial composition and abundance change as soil variables and potential moisture availability change with drier sites exhibiting lower cover and species richness. This study confirms the importance of substrate properties on plant water availability. Results from both techniques reveal that subtle differences in substrate texture and age may lead to large differences in plant available water, thereby impacting plant community structure.

INTRODUCTION

Hamerlynck and McAuliffe 2010). Reynolds et al. (2004) note that productivity in deserts is not a direct response to rainfall but rather to soil water availability.


Martinez et al. 2004, Poulos et al. 2007). For example, soil particle sorting down fan and bajada gradients has been well documented. Upper bajadas have been found to have a higher proportion of large, coarse soil particles, and a lower salinity than the lower portions of bajadas (Phillips and MacMahon 1978, MacMahon and Schimpf 1981, MacMahon and Wagner 1985, Bowers and Lowe 1986, Parker 1995). Soil particle size greatly affects evaporative water loss and water availability for desert plants (MacMahon and Schimpf 1981). Upper bajadas with larger soil particles tend to allow water to percolate lower in the profile, thus making more water available later in the dry season when it may be limiting; therefore, upper bajadas have been found to have greater species richness and diversity (Key et al. 1984). While the occurrence of soil particle sorting on bajada gradients has been well established, this model works as a generalization and tends to oversimplify the complexities of specific soil, geologic, and topographic variables.

Although it is known that soil, geology, topography, and bioclimatic factors affect the structure of arid plant communities, the relative contribution of these factors remains unclear. This study will examine the abiotic factors influencing plant community structure in a Mojave Desert ecosystem. Specifically, we will investigate the role of parent material, soil, geology, topography, and climate variables in shaping plant species composition and abundance. In order to disentangle the influence of each of these abiotic variables, two fundamentally different multivariate ordination techniques were used to examine patterns in species composition and abundance. Ordination is often used as an exploratory data-analysis technique that seeks pattern or structure in a multivariate dataset and may reveal how species composition varies with environmental factors. The
ideal ordination technique is able to determine the most important dimensions (or gradients) in a data set, and ignore "noise" or chance variation (Whittaker 1978, Gauch 1982, Austin 1985, Jongman et al. 1995, McGarigal et al. 2000, McCune and Grace 2002).

Numerous studies use a combination of direct and indirect methods and compare the results of each technique for consistency (R. del Morel et al. 1995, Ohmann and Spies 1998, El-Ghani and Amer 2003, Jafari 2004, He et al. 2007, Canadas et al. 2010). To our knowledge, there have been no studies which have compared direct and non-direct methods in the Mojave Desert. We expect to see vegetation patterns change as soil variables and thus potential moisture availability change. We predict that sites characterized by soils with smaller particle sizes will be the driest sites and exhibit lower cover and species richness.

Given that deserts cover approximately one fifth of the Earth’s surface, approximately 777,000 km² in North America (MacMahon 1987, 2001), and desert cities in the southwestern United States are experiencing unprecedented levels of human population growth and expansion (Webb et al. 2009, United States Census 2014), identifying the relationships among plant communities and the abiotic variables driving their structure is critical to understanding the desertification process that is occurring globally and for making restoration and management decisions in these fragile systems.
METHODS

Study area

The Upper Las Vegas Wash Conservation Transfer Area (ULVWCTA), Nevada, consists of a 7,400 ha land parcel of Mojave Desert vegetation on alluvial fan (bajada) and basin floor deposits derived from the Spring and Sheep Mountains. The area sits north of Las Vegas and is transected by a complex of Pleistocene spring deposits and their attendant washes. A research team from Utah State University was tasked with creating vegetation and soil maps of the ULVWCTA. This work was initiated in July 2006.

Vegetation sampling

A stratified sampling design was used to collect data for describing the ULVWCTA vegetation and developing a vegetation map. Two strata, based on broad geomorphic categories, were identified. The first was defined as alluvial fan/wash and totaled 5,270 ha (71%) of the ULVWCTA. The second stratum (2,130 ha, 29%) was defined as basin floor/spring deposit, and was associated with past ground-water discharge (evidenced by highly calcareous spring deposits) and lacustrine sediments.

A total of 240 plots were sampled across the ULVWCTA. Initially, the mapping data consisted of 163 sample plots that were systematically distributed along 13 north-south transects spaced 2000 meters apart. Vegetation data were collected every 100 meters in the basin floor/spring deposit stratum and every 500 meters in the alluvial fan/wash stratum. Preliminary evaluation of these data indicated inadequate coverage of the area, so an additional 77 sample plots were established and surveyed to increase
sampling intensity where vegetation variation was greater, and where spectral reflectance
data from Landsat 7 and ASTER satellites suggested greater complexity in geomorphic
surfaces and vegetation.

Each sample plot consisted of the area of a circle with a 10-m radius. Each
circular plot was divided into quarters by an east-west and a north-south line. One
quarter of each plot was used to survey vegetation. The quarter chosen for sampling was
rotated in a clockwise manner from one sample plot to the next. Vegetation data were
collected for woody perennials only. For each plant within the sample quarter, the
height, width in two directions (the longest width and the width perpendicular to this),
and species were recorded.

Sampling data were used to create a detailed vegetation map for the area
(methodology described in MacMahon et al. 2008). Seven associations were identified
and described in addition to heavily disturbed areas defined as “human modified”
(MacMahon et al. 2008). Table 2.1 provides a list and description of each association.
This map, in addition to specific plant measurements, provided the vegetation data for the
analyses. A list of identified plants species can be found in Appendix A.

Soil sampling, geologic data, and topographic data

A refined soil map (MacMahon et al. 2008) was created for the ULVWCTA. The
map was based on the most recent, publicly available soil survey data for the area
produced by the US Department of Agriculture Natural Resources Conservation Service.
Refinement was based on high-resolution aerial photography, a digital terrain model,
spectral imagery, and 45 soil pedons. There was a minimum of two pedon locations per
refined soil map unit and a minimum of two per vegetation map unit. Eight soil map
units were identified for the area. Table 2.2 provides a list and description of each unit. This map provided the soil data for the analyses.

Geologic data were obtained from a USGS map (1:100,000 Geologic and Geophysical maps of the Las Vegas 30’ X 60’ Quadrangle, Clark and Nye Counties, Nevada, and Inyo County, California (Page et al. 2005). Table 2.3 provides a list and description of each unit. This map provided the geologic data for the analyses.

Slope, elevation, and aspect were determined from high-resolution aerial photography and a topographic contour map derived from the digital terrain model and spectral imagery. Slope data were transformed into a continuous north-south gradient and east-west gradient by using the sine and cosine transformations (Guisan et al. 1999).

**Climate data**

Climate data were derived using DAYMET (Daily Surface Weather Data and Climatological Summaries). DAYMET is a model that generates daily surfaces of temperature, precipitation, humidity, and radiation over large regions of complex terrain. It was developed to fulfill the need for fine resolution, daily meteorological and climatological data necessary for plant growth model inputs (Thornton et al. 1997). The DAYMET model provided 156 variables which consisted of monthly means for thirteen different climate factors. These factors included maximum and minimum temperatures, average daytime temperatures, relative humidity, ambient and saturated vapor pressure, precipitation, evapotranspiration, solar radiation, and a moisture index. In order to reduce the dataset and eliminate correlations among the monthly values, Principle Components Analysis (PCA) was carried out on each of the climate variables using with SAS 9.2 for Windows (SAS, 2011). Most of the variables were condensed into a single principal
component which explained 75% - 95% of the variability for each set of monthly variables.

Although PCA was used to reduce the monthly values for each variable down to one or two principal components, Pearson Correlation Coefficients revealed that many of these reduced variables were still correlated in the manner in which they changed over the year. The principal components for maximum, minimum, and average daytime temperatures were all positively correlated. In addition, these were all positively correlated with vapor pressure components. All of these components were negatively correlated with precipitation variables. Evapotranspiration and the moisture index were negatively correlated. Evapotranspiration was moderately correlated with the temperature and vapor pressure components while the moisture index had a moderate negative correlation with these. Solar radiation components were moderately positively correlated with evapotranspiration and moderately negatively correlated with the moisture index. Because so many of the variables were highly correlated, only daytime temperature, direct solar radiation, and evapotranspiration were kept in the final analysis.

**Analytical methods**

There are two approaches to ordination, direct and indirect gradient analysis (Whittaker 1967, Whittaker 1978, Gauch 1982, Austin 1985, ter Braak 1987, ter Braak and Prentice 1988, ter Braak 1994, McCune and Grace 2002). Direct gradient analysis involves arranging samples by positions along one or more environmental gradients. It utilizes environmental data in addition to species data and reveals whether or not species composition is related to the measured environmental variables. Indirect gradient analysis uses species data only. Indirect gradient analysis organizes samples based on association
among the species. The species’ patterns reflect environmental gradients without measuring them by assuming plants which are grouped together respond to the environment similarly. Indirect gradient analysis may reveal environmental influences that have not been measured (McCune and Grace, 2002). With this approach, any information about the environment should be used after the analysis as an interpretative tool.

In order to assess the degree to which abiotic variables influence plant associations of the ULVWCTA, species cover values were analyzed with the DAYMET PCA variables, geologic (Page et al. 2005), topographic, and refined soil (MacMahon et al. 2008) datasets using both direct and indirect non-linear techniques. Nonmetric Multidimensional Scaling (NMDS) was used for the indirect analysis while Canonical Correspondence Analysis (CCA) was used for the direct analysis. Using the Bray-Curtis coefficient with NMDS has been described as a robust technique when the objective is to recover underlying environmental gradients (Minchin 1987). CCA has been noted as a superior method with complex sampling designs, skewed distributions, and community data that contain many zeros (ter Braak 1987, Palmer 1993). Analyses were performed in the Vegan R package (Oksanen et al. 2011).

All environmental data were entered into a Geographic Information System (GIS). The GIS was used to generate a spreadsheet for analysis. The spreadsheet was organized by plot with corresponding soil, geology, parent material, vegetation association, climate, and topographic descriptors. Appendix B provides a table of each plot and its attendant soil map unit, vegetation association, geologic unit, and elevation (Table B.1). Species cover data was organized into a separate spreadsheet in a species by
plot matrix. Appendix C provides a table listing the plant species found in each plot, the total number of individuals found in each plot, and the total cover for each species. Plots devoid of plant material or species that occurred in less than 5% of the samples were omitted from the analyses (Gauch 1982, Shupe 2005). The results from the direct and indirect gradient analyses were compared for consistency.

RESULTS

NMDS. The NMDS ordination was conducted using the metaMDS function in the Vegan library (version 2.0-0, Oksanen et al. 2011) for R (version 2.13.2; R Development Core Team, Vienna, Austria) based on Bray-Curtis dissimilarity and 500 random starts. A solution with three axes was selected based on visual inspection of a scree plot of stress values. The scree plot can be found in Appendix D (Figure D.1). The two dimensional solution produced a stress value of 0.175 while the three dimensional solution had a stress value of 0.126. There was no clear “elbow” between the two and three axes solutions. McCune and Grace (2002) mentioned that most ecological community data sets have solutions with stress values between 0.10 and 0.20. While values in the lower half of this range are satisfactory, values approaching 0.20 may be cause for concern. Therefore, the three dimensional solution was chosen. It should be noted that the orientation of NMDS axes are arbitrary and one axis does not hold more weight than any other. Ordination diagrams arrange variables so as the distance between points corresponds with the dissimilarity between sites. Larger distances are most accurate (ter Braak 1994).
The first NMDS axis identifies a clear distinction between parent material and the soil, climatic conditions, and species associated with each. Species growing on hot, dry spring and basin floor deposits (*Atriplex confertifolia, Ephedra torreyana, Menodora spinescens*) with shallow soil (Las Vegas soil), with low hydraulic conductivity, and very low available water capacity had a strong positive correlation to the first axis. The monthly average daytime temperature was also positively correlated, indicating that temperature increases at this end of the gradient. The cacti species, *Cylindropuntia echinocarpa* and *Opuntia basilaris*, growing on bajada alluvium at higher elevations were negatively correlated with the first axis. Figure 2.1 displays axes one and two and Figure 2.2 displays axes one and three. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Table 2.4 provides the coordinates for each variable along each axis. In order to keep the figures uncluttered, only the species and significant climate variables are displayed. Ordination graphics for each categorical variable (vegetation association, geologic unit, and soil association) are provided in Appendix E (Figures E.1 – E.6). Table E.1. shows the coordinates for each plot along each axis.

The second NMDS axis depicts a richness and cover gradient within the basin floor sites. Higher daytime temperature, higher potential evapotranspiration, and geology associated with fine-grained, calcareous deposits associated with past-ground water discharge (geology unit Qsu) were positively correlated with the second NMDS axis. In addition, *Atriplex confertifolia* and *Larrea tridentata* and sites where they occur in low density as the sole species were positively correlated with this axis. The *Ambrosia dumosa – Menodora spinescens* association and species found in this association
(Xyloriza tortifolia, Menodora spinescens, and Ephedra nevadensis) were negatively correlated. The *Ambrosia dumosa – Menodora spinescens* association also occurs on fine-grained, calcareous deposits associated with past-ground water discharge (primarily Qscd), but has the greatest species richness (richness = 17) and mean plant density (9502 n/ha) of all communities associated with the basin floor or Las Vegas and Las Vegas-Destazo complex soils. NMDS axis two confirms that basin floor sites that experience higher monthly average daytime temperature and higher potential evapotranspiration exhibit lower species richness. Soils, vegetation associations, and species associated with alluvium do not influence this gradient (i.e., they sit in the middle of the axis). Figure 2.1 displays axes one and two and Figure 2.3 displays axes two and three. Ordination graphics for each categorical variable (vegetation association, geologic unit, and soil association) are provided in Appendix E (Figures E.1 – E.3 and E.7 – E.9).

The third NMDS axis consists of a richness and cover gradient within the alluvium sites. Direct solar radiation, evaporation, and species that grow on open, flat, alluvial sites (*Opuntia basilaris, Ephedra torreyana, Krameria erecta*) were negatively correlated with the third NMDS axis, whereas species associated with active wash areas (*Hymenoclea salsola, Encelia virginensis, Atriplex polycarpa, Gutierrezia* species) were positively correlated. This axis represents the gradient between plants with greater cover growing in active washes versus flat, open sites where plants have less cover and lose more moisture via direct solar radiation and evapotranspiration. This axis represents variation within alluvium sites. Soils, vegetation associations, and species associated with the basin floor/spring deposits do not influence this gradient (i.e., they sit in the middle of the axis). Figure 2.2 displays axes one and three and Figure 2.3 displays axes
two and three. Ordination graphics for each categorical variable (vegetation association, geologic unit, and soil association) are provided in Appendix E (Figures E.4 – E.9).

CCA. The CCA was initially run with all of the environmental variables. Permutation tests were run to determine which variables were significant. The tests were performed three times, reducing the number of variables each iteration. The variables run in the fourth iteration were kept in the final analysis: average temperature, direct solar radiation, soil, and vegetation association variables. Constrained variation is the variation that is explained by the axes in the CCA (0.3318 or 33.185\%). Eigenvalues for the first two axes were 0.5114, and 0.1560 (accounting for 55.83\% and 17.03\% of the variation).

The CCA analysis presents trends similar, but not identical, to the NMDS analysis. The first CCA axis, which accounts for over half of the explained variation in the analysis, depicts a moisture, parent material, and plant cover gradient. Species, vegetation associations, and soils associated with alluvium in active wash areas (the *Atriplex polycarpa - Ambrosia dumosa* Association, *Atriplex polycarpa*, *Hymenoclea salsola*, and Arizo soil) were positively correlated with the first CCA axis. Species, vegetation associations, and soils associated with dry basin floor/spring deposit sites (e.g., *Menodora spinescens*, the Las Vegas-DeStazo soil complex, the *Ambrosia dumosa - Menodora spinescens* Association, the *Ambrosia dumosa - Atriplex confertifolia* Association, and the Las Vegas and Badlands soils) were negatively correlated. The *Atriplex polycarpa - Ambrosia dumosa* Association shows the greatest mean plant density (4269 n/ha) of all communities associated with the alluvium parent material and the *Ambrosia dumosa - Menodora spinescens* Association has the greatest and mean plant
density (9502 n/ha) of all communities associated with the basin floor. Table 2.5 provides the coordinates for each variable along this axis. Figure 2.4 displays the ordination diagram. Appendix F provides the coordinates for each plot in the CCA analysis (Table F.1).

The second CCA axis is correlated with parent material and soil. Soils and vegetation communities associated with fine-grained basin floor were positively correlated with the second CCA axis (e.g., the Las Vegas soil, the *Ambrosia dumosa - Atriplex confertifolia* Association, the Las Vegas-DeStazo soil complex, and the *Ambrosia dumosa - Menodora spinescens* Association). Sites with Las Vegas soil, and Qscd geology that support only a few *Atriplex confertifolia* individuals sit at the extreme positive end of this gradient. The alluvium soil, Weiser, and cacti species associated with gravelly bajada soil (*Cylindropuntia echinocarpa* and *Opuntia basilaris*) were negatively correlated. Table 2.5 provides the coordinates for each variable along this axis. Figure 2.4 displays the ordination diagram.

**DISCUSSION**

The soils of the ULVWTA can be broadly split into two geomorphic categories: alluvial fan/wash and basin floor/spring deposit. The alluvial fan/wash soils are typically dominated by relatively coarse-textured alluvium. Soil map units include Weiser, Dalian-McCullogh Complex, Weiser-Wechech Association, and Arizo. Geologic map units associated with alluvial fans/washes include Qay, Qayo, and Qayy. Vegetation associations include the *Larrea tridentata - Ambrosia dumosa* Association, *Atriplex*

Basin floor soils are generally finer textured alluvium and spring deposits, and typically have horizons and/or nodules cemented with carbonates (calcite). These areas are associated with past ground water discharge and include the Las Vegas and Las Vegas-Destazo Complex soil map units. The prominent geologic unit is Qscd and vegetation associations include Ambrosia dumosa - Atriplex confertifolia Association, Ambrosia dumosa - Menodora spinescens Association, Badlands, and the Larrea tridentata Association. The basin floor is generally hotter, drier, and lower in elevation than the alluvial fan/wash.

Both the NMDS and CCA results reveal a dichotomy between basin floor/spring deposit and alluvial fan/wash and the soils, species, and vegetation communities within each. In addition, each multivariate technique revealed the gradients within each geomorphic category. The second NMDS axis depicted a richness and cover gradient within the basin floor sites, whereas the third axis showed the same pattern in the alluvial fan/wash sites. All of these patterns are produced from variations in water availability resulting from differences in soil texture, degree of carbonate cementation, and horizon development. This is visually apparent when comparing basin floor and alluvial fan/wash soils but more subtle while observing each geologic unit on its own. The NMDS elucidated the subtle patterns within each geomorphic unit while the CCA revealed patterns between geomorphic units. While CCA is constrained by the environmental variables provided in the analysis the NMDS is free to find whatever compositional trend may exist.
The patterns revealed in the gradient analyses were consistent with our prediction that vegetation characteristics change as soil variables and potential moisture availability change with drier sites exhibiting lower cover and species richness. They also support the well cited relationship between soil texture, age, and horizon development and its role in water availability. At the largest scale, we observed that elevation and parent material dictate moisture availability. Higher elevation alluvial fans (bajadas) are coarser textured, and potentially have more moisture availability than the finer textured, lower elevation basin floor (playas) which also has a greater degree of cementation by carbonates. Because of soil texture differences and the associated water holding capacities, alluvial fans/washes accommodated plant communities with greater diversity and cover than basin floor sites. This observation is consistent with literature citing age-dependent soil profile development as one of the strongest predictors of plant community composition in arid environments (Hamerlynch et al 2002) with younger soils having more water available than older soils (McAuliffe 1994, Nimmo 2009), upper bajadas and coarse soils having greater species richness (Barbor and Diaz 1973, Key et al. 1984), and soil particle sorting down bajada fans with upper bajadas having a higher proportion of larger soil particles than lower bajadas (Phillips and MacMahon 1978, MacMahon and Schimpf 1981, MacMahon and Wagner 1985, Key et al. 1984, Bowers and Lowe 1986, Parker 1995).

While the classic bajada gradient model has played a vital role in understanding arid vegetation patterns, it may oversimplify the complexities and contribution of specific soilmap unit. The topography and parent material in arid regions is heterogeneous, resulting in considerable spatial variation in soils (McAullife 1994, Smith et al. 1995).
Perhaps the gradient model applies broadly from the bajada to playa or within a soil map unit, but soil and landscape characteristics may change abruptly. Webb et al. (2009) describe soils as mosaics. While the gradient hypothesis largely ignores the fact that there are different soils with different ages and pedogenic factors that may change soil hydraulic properties, the soil mosaic approach recognizes that soils are distinct and vegetation will respond accordingly. Our GIS approach and the geopedological approach used by Michaud et al. (2013) are useful to describe the relationship between vegetation, soil, parent material, geology, and climate and explore the soil mosaic hypothesis. GIS overlays of geology, soil, and vegetation maps, and digital elevation models will allow researchers to explore the value of soil mosaic hypotheses at multiple scales.

It is well documented and observed in our study that variations in soil type govern plant community characteristics. Rather than limiting our view to the bajada gradient we should look at the landscape as a soil mosaic and consider this mosaic when developing monitoring and management activities. While the gradient model will provide generalities as to texture and age across a landscape, the soil mosaic hypothesis will provide details. A soils map will provide insight into the factors that control each vegetation community and is essential to understanding desert ecosystem processes.

ACKNOWLEDGMENTS

Funding for this research was provided by USDI Bureau of Land Management. Special thanks to Gayle Marrs-Smith at the Las Vegas Field Office for assistance. Statistical support was provided by Dr. Jari Oksanen, Dr. David Roberts, and Susan Durham. GIS/database support was provided by Glen Busch.


Table 2.1. Vegetation associations of the ULVWCTA.

<table>
<thead>
<tr>
<th>Vegetation Association</th>
<th>Description</th>
<th>Area (ha)</th>
<th>Elevation (m)</th>
<th>Number of plots sampled</th>
<th>Richness</th>
<th>Density (n/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Larrea tridentata</em> - <em>Ambrosia dumosa</em> Association</td>
<td><em>Larrea tridentata</em> and <em>Ambrosia dumosa</em> compose ≥70% of the relative density</td>
<td>5,817</td>
<td>659 to 929</td>
<td>143</td>
<td>34</td>
<td>3889</td>
</tr>
<tr>
<td><em>Larrea tridentata</em> Association</td>
<td><em>Larrea tridentata</em> is the dominant shrub and these areas coincide with basin floor soils</td>
<td>286</td>
<td>729 to 828</td>
<td>11</td>
<td>7</td>
<td>463</td>
</tr>
<tr>
<td><em>Atriplex polycarpa</em> - <em>Ambrosia dumosa</em> Association</td>
<td><em>Atriplex polycarpa</em> and <em>Ambrosia dumosa</em> dominate in wet, active, and dry washes</td>
<td>245</td>
<td>658 to 831</td>
<td>19</td>
<td>14</td>
<td>4269</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Menodora spinescens</em> Association</td>
<td><em>Ambrosia dumosa</em> and <em>Menodora spinescens</em> make up the greatest shrub density in the basin floor</td>
<td>42</td>
<td>667 to 715</td>
<td>8</td>
<td>17</td>
<td>9502</td>
</tr>
<tr>
<td>Badlands</td>
<td>barren ground with some <em>Larrea tridentata</em></td>
<td>94</td>
<td>705 to 742</td>
<td>6</td>
<td>4</td>
<td>276</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Larrea tridentata</em>: Upper Alluvial Fan Association</td>
<td><em>Ambrosia dumosa</em> in association with <em>Larrea tridentata</em> make up the greatest density on the upper alluvial fan</td>
<td>36</td>
<td>798 to 876</td>
<td>8</td>
<td>12</td>
<td>2674</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Atriplex confertifolia</em> Association</td>
<td><em>Ambrosia dumosa</em> in association with <em>Atriplex confertifolia</em> characterize this association in the basin floor/spring deposit</td>
<td>445</td>
<td>659 to 724</td>
<td>41</td>
<td>14</td>
<td>2612</td>
</tr>
</tbody>
</table>
Table 2.2: Soil map units of the ULVWCTA.

<table>
<thead>
<tr>
<th>Soil</th>
<th>Parent material</th>
<th>Landform</th>
<th>Drainage class</th>
<th>(Ksat)*</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizo</td>
<td>Mixed alluvium</td>
<td>Channels</td>
<td>Excessively drained</td>
<td>High to very high (5.95 to 19.98 in/hr)</td>
<td>Very gravelly loamy sand</td>
</tr>
<tr>
<td>Dalian-McCullough Complex</td>
<td>Alluvium derived from limestone and dolostone</td>
<td>Fan skirts</td>
<td>Well drained</td>
<td>High (1.98 to 5.95 in/hr)</td>
<td>Very gravelly fine sandy loam</td>
</tr>
<tr>
<td>Las Vegas</td>
<td>Alluvium derived from limestone</td>
<td>Basin-floor remnants</td>
<td>Well drained</td>
<td>Very low (0 in/hr)</td>
<td>Gravelly fine sandy loam</td>
</tr>
<tr>
<td>Las Vegas-DeStazo Complex</td>
<td>Alluvium derived from limestone</td>
<td>Alluvial flats</td>
<td>Well drained</td>
<td>Very low (0 in/hr)</td>
<td>Gravelly fine sandy loam</td>
</tr>
<tr>
<td>Weiser-Wechech Association</td>
<td>Alluvium derived from limestone and dolomite</td>
<td>Fan remnants</td>
<td>Well drained</td>
<td>Moderately high to high (0.57 to 5.95 in/hr)</td>
<td>Extremely gravelly fine sandy loam</td>
</tr>
<tr>
<td>Weiser</td>
<td>Alluvium derived from limestone and dolomite</td>
<td>Fan remnants</td>
<td>Well drained</td>
<td>High (1.98 to 5.95 in/hr)</td>
<td>Extremely gravelly fine sandy loam</td>
</tr>
<tr>
<td>Weiser-Goodsprings Complex</td>
<td>Alluvium derived from limestone and dolomite</td>
<td>Fan remnants</td>
<td>Well drained</td>
<td>High (1.98 to 5.95 in/hr)</td>
<td>Extremely gravelly fine sandy loam</td>
</tr>
<tr>
<td>Badland</td>
<td>Mixed alluvium over lacustrine</td>
<td>Hills on alluvial flats</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Ksat=capacity of the most limiting layer to transmit water
Table 2.3: Geologic units of the ULVWCTA.

<table>
<thead>
<tr>
<th>Unit*</th>
<th>Parent Material</th>
<th>Age</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Qai</td>
<td>Intermediate fan alluvium</td>
<td>Late and middle Pleistocene</td>
<td>Cemented alluvial-fan gravel, with interbedded sand; poorly to moderately well sorted</td>
</tr>
<tr>
<td>Qay</td>
<td>Young fan alluvium</td>
<td>Holocene and latest Pleistocene</td>
<td>Noncemented alluvial-fan gravel and sand with weakly developed soil.</td>
</tr>
<tr>
<td>Qayo</td>
<td>Older young alluvium</td>
<td>Holocene and latest Pleistocene</td>
<td>Noncemented gravel and sand with weakly developed soil of alluvial-fan remnants</td>
</tr>
<tr>
<td>Qayy</td>
<td>Youngest alluvium</td>
<td>Holocene</td>
<td>Noncemented alluvial-fan gravel and sand of intermittently active wash complexes</td>
</tr>
<tr>
<td>Qfy</td>
<td>Intermittently active fluvial fine-grained alluvium</td>
<td>Late Holocene</td>
<td>Brown to gray sand, silt, mud, and interbedded gravel.</td>
</tr>
<tr>
<td>Qscd</td>
<td>Intermediate fine-grained deposits associated with past ground-water discharge</td>
<td>Late Pleistocene</td>
<td>Top 1-2 m is characteristically resistant light-gray calcareous mud that is partially cemented with calcite</td>
</tr>
<tr>
<td>Qsu</td>
<td>Undivided young and intermediate fine-grained deposits associated with past ground-water discharge</td>
<td>Early Holocene and late Pleistocene</td>
<td>Light-gray to light-brown unconsolidated silt, sandy silt, silty sand, and mud or the top 1-2 m is characteristically resistant light-gray calcareous mud that is partially cemented with calcite</td>
</tr>
</tbody>
</table>

*Unit= map unit
Table 2.4. Three-dimensional NMDS results. The table provides coordinates for each variable examined in the NMDS analysis (obtained from a three dimensional ordination diagram). The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate.

<table>
<thead>
<tr>
<th>NMDS Climate variables</th>
<th>NMDS 1</th>
<th>NMDS 2</th>
<th>NMDS 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monthly average daytime temperature (DAYTEMP)</td>
<td>0.71</td>
<td>0.70</td>
<td>-0.10</td>
</tr>
<tr>
<td>Potential evapotranspiration (EVAP)</td>
<td>0.15</td>
<td>0.51</td>
<td>-0.85</td>
</tr>
<tr>
<td>Direct solar radiation (DIRECTSR)</td>
<td>-0.43</td>
<td>-0.10</td>
<td>-0.90</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>NMDS Species Variables</th>
<th>NMDS 1</th>
<th>NMDS 2</th>
<th>NMDS 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ambrosia dumosa</td>
<td>-0.23</td>
<td>-0.23</td>
<td>0.11</td>
</tr>
<tr>
<td>Atriplex confertifolia</td>
<td>1.47</td>
<td>0.78</td>
<td>0.05</td>
</tr>
<tr>
<td>Atriplex polycarpa</td>
<td>-0.32</td>
<td>0.31</td>
<td>1.22</td>
</tr>
<tr>
<td>Cylindropuntia echinocarpa</td>
<td>-0.62</td>
<td>-0.42</td>
<td>-0.51</td>
</tr>
<tr>
<td>Encelia virginensis</td>
<td>-0.29</td>
<td>-0.63</td>
<td>1.26</td>
</tr>
<tr>
<td>Ephedra nevadensis</td>
<td>0.55</td>
<td>-0.78</td>
<td>0.21</td>
</tr>
<tr>
<td>Ephedra torreyana</td>
<td>1.21</td>
<td>-0.17</td>
<td>-0.34</td>
</tr>
<tr>
<td>Gutierrezia species</td>
<td>-0.04</td>
<td>-0.53</td>
<td>1.22</td>
</tr>
<tr>
<td>Hymenoclea salsola</td>
<td>-0.49</td>
<td>-0.04</td>
<td>2.00</td>
</tr>
<tr>
<td>Krameria erecta</td>
<td>0.00</td>
<td>-0.57</td>
<td>-0.44</td>
</tr>
<tr>
<td>Larrea tridentata</td>
<td>-0.48</td>
<td>0.43</td>
<td>-0.11</td>
</tr>
<tr>
<td>Lycium andersonii</td>
<td>0.73</td>
<td>-0.20</td>
<td>0.31</td>
</tr>
<tr>
<td>Menodora spinescens</td>
<td>1.03</td>
<td>-0.81</td>
<td>-0.18</td>
</tr>
<tr>
<td>Opuntia basilaris</td>
<td>-0.69</td>
<td>-0.05</td>
<td>-0.90</td>
</tr>
<tr>
<td>Psorothamnus fremontii</td>
<td>0.11</td>
<td>-0.54</td>
<td>0.07</td>
</tr>
<tr>
<td>Xylorhiza tortifolia</td>
<td>-0.03</td>
<td>-1.43</td>
<td>0.55</td>
</tr>
<tr>
<td>Yucca schidigera</td>
<td>-0.31</td>
<td>-0.57</td>
<td>0.01</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>NMDS Soil Variables</th>
<th>NMDS 1</th>
<th>NMDS 2</th>
<th>NMDS 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizo</td>
<td>-0.27</td>
<td>0.04</td>
<td>0.48</td>
</tr>
<tr>
<td>Badland</td>
<td>0.09</td>
<td>0.28</td>
<td>-0.03</td>
</tr>
<tr>
<td>Dalian-McCullough Complex</td>
<td>-0.21</td>
<td>-0.01</td>
<td>-0.03</td>
</tr>
<tr>
<td>Las Vegas-DeStazo Complex</td>
<td>0.63</td>
<td>-0.07</td>
<td>-0.06</td>
</tr>
<tr>
<td>Las Vegas</td>
<td>1.06</td>
<td>0.40</td>
<td>0.00</td>
</tr>
<tr>
<td>Weiser</td>
<td>-0.30</td>
<td>0.08</td>
<td>-0.23</td>
</tr>
<tr>
<td>Weiser-Wechech Association</td>
<td>-0.10</td>
<td>-0.26</td>
<td>-0.04</td>
</tr>
</tbody>
</table>

(Continued on next page)
Table 2.4. Three-dimensional NMDS results (continued).

<table>
<thead>
<tr>
<th>NMDS Vegetation Association Variables</th>
<th>NMDS 1</th>
<th>NMDS 2</th>
<th>NMDS 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Atriplex confertifolia</em> Association</td>
<td>0.99</td>
<td>0.28</td>
<td>-0.02</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Larrea tridentata</em> Association</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper Alluvial Fan Association</td>
<td>0.11</td>
<td>0.00</td>
<td>0.22</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Menodora spinescens</em> Association</td>
<td>0.55</td>
<td>-0.46</td>
<td>-0.01</td>
</tr>
<tr>
<td><em>Atriplex polycarpa</em> - <em>Ambrosia dumosa</em> Association</td>
<td>-0.24</td>
<td>0.17</td>
<td>0.78</td>
</tr>
<tr>
<td>Badlands</td>
<td>-0.20</td>
<td>-0.31</td>
<td>-0.23</td>
</tr>
<tr>
<td><em>Larrea tridentata</em> Association</td>
<td>-0.43</td>
<td>0.68</td>
<td>-0.16</td>
</tr>
<tr>
<td><em>Larrea tridentata</em> - <em>Ambrosia dumosa</em> Association</td>
<td>-0.25</td>
<td>-0.12</td>
<td>-0.09</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>NMDS Geologic Unit Variables</th>
<th>NMDS 1</th>
<th>NMDS 2</th>
<th>NMDS 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Qai</td>
<td>-0.32</td>
<td>-0.38</td>
<td>0.34</td>
</tr>
<tr>
<td>Qay</td>
<td>-0.25</td>
<td>-0.13</td>
<td>-0.16</td>
</tr>
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<td>Qayo</td>
<td>0.22</td>
<td>-0.23</td>
<td>0.04</td>
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<td>Qayy</td>
<td>-0.31</td>
<td>0.05</td>
<td>0.37</td>
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<tr>
<td>Qfy</td>
<td>-0.37</td>
<td>0.17</td>
<td>-0.09</td>
</tr>
<tr>
<td>Qscd</td>
<td>0.51</td>
<td>0.21</td>
<td>-0.02</td>
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<tr>
<td>Qsu</td>
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<td>0.74</td>
<td>-0.15</td>
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<table>
<thead>
<tr>
<th>NMDS Parent Material Variables</th>
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<th>NMDS 2</th>
<th>NMDS 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>alluvium</td>
<td>-0.21</td>
<td>-0.09</td>
<td>0.02</td>
</tr>
<tr>
<td>spring deposit</td>
<td>0.62</td>
<td>0.19</td>
<td>-0.02</td>
</tr>
<tr>
<td>spring deposit and alluvium</td>
<td>-0.18</td>
<td>0.17</td>
<td>-0.07</td>
</tr>
</tbody>
</table>
Table 2.5. CCA results. The table provides coordinates for each variable examined in the CCA analysis (obtained from the ordination diagram). The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate.

<table>
<thead>
<tr>
<th>CCA Soil Variables</th>
<th>CCA1</th>
<th>CCA2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizo</td>
<td>1.54</td>
<td>0.04</td>
</tr>
<tr>
<td>Badland</td>
<td>-0.09</td>
<td>-0.05</td>
</tr>
<tr>
<td>Dalian-McCullough complex</td>
<td>-0.42</td>
<td>-0.11</td>
</tr>
<tr>
<td>Las Vegas-DeStazo complex</td>
<td>-0.58</td>
<td>2.63</td>
</tr>
<tr>
<td>Las Vegas</td>
<td>-0.57</td>
<td>3.03</td>
</tr>
<tr>
<td>Weiser</td>
<td>-0.28</td>
<td>-0.84</td>
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<tr>
<td>Weiser-Wechech association</td>
<td>-0.46</td>
<td>-0.12</td>
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</table>

<table>
<thead>
<tr>
<th>CCA Vegetation Association Variables</th>
<th>CCA1</th>
<th>CCA2</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Atriplex confertifolia</em> Association</td>
<td>-0.57</td>
<td>3.01</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Larrea tridentata</em>: Upper Alluvial Fan Association</td>
<td>-0.57</td>
<td>0.54</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Menodora spinescens</em> Association</td>
<td>-0.58</td>
<td>2.62</td>
</tr>
<tr>
<td><em>Atriplex polycarpa</em> - <em>Ambrosia dumosa</em> Association</td>
<td>2.36</td>
<td>0.15</td>
</tr>
<tr>
<td>Badlands</td>
<td>-0.50</td>
<td>-0.25</td>
</tr>
<tr>
<td><em>Larrea tridentata</em> Association</td>
<td>-0.42</td>
<td>-0.65</td>
</tr>
<tr>
<td><em>Larrea tridentata</em> - <em>Ambrosia dumosa</em> Association</td>
<td>-0.39</td>
<td>-0.41</td>
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<table>
<thead>
<tr>
<th>CCA Species Variables</th>
<th>CCA1</th>
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</tr>
</thead>
<tbody>
<tr>
<td><em>Ambrosia dumosa</em></td>
<td>-0.26</td>
<td>0.09</td>
</tr>
<tr>
<td><em>Atriplex confertifolia</em></td>
<td>-0.45</td>
<td>2.20</td>
</tr>
<tr>
<td><em>Atriplex polycarpa</em></td>
<td>2.13</td>
<td>0.08</td>
</tr>
<tr>
<td><em>Cylindropuntia echinocarpa</em></td>
<td>-0.38</td>
<td>-0.72</td>
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<tr>
<td><em>Encelia virginensis</em></td>
<td>1.30</td>
<td>-0.03</td>
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<td><em>Ephedra nevadensis</em></td>
<td>-0.50</td>
<td>0.44</td>
</tr>
<tr>
<td><em>Ephedra torreyana</em></td>
<td>-0.49</td>
<td>1.53</td>
</tr>
<tr>
<td><em>Gutierrezia species</em></td>
<td>1.15</td>
<td>0.43</td>
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<td><em>Hymenoclea salsola</em></td>
<td>2.07</td>
<td>0.20</td>
</tr>
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<td><em>Krameria erecta</em></td>
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<td>0.14</td>
</tr>
<tr>
<td><em>Larrea tridentata</em></td>
<td>-0.17</td>
<td>-0.27</td>
</tr>
<tr>
<td><em>Lycium andersonii</em></td>
<td>-0.22</td>
<td>1.00</td>
</tr>
<tr>
<td><em>Menodora spinescens</em></td>
<td>-0.59</td>
<td>2.52</td>
</tr>
<tr>
<td><em>Opuntia basilaris</em></td>
<td>-0.46</td>
<td>-0.56</td>
</tr>
<tr>
<td><em>Psorothamnus fremontii</em></td>
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<td>0.07</td>
</tr>
<tr>
<td><em>Xylorhiza tortifolia</em></td>
<td>-0.50</td>
<td>0.90</td>
</tr>
<tr>
<td><em>Yucca schidigera</em></td>
<td>-0.45</td>
<td>-0.17</td>
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</table>

<table>
<thead>
<tr>
<th>CCA Climate Variables</th>
<th>CCA1</th>
<th>CCA2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average daytime temperature (AVETEMP)</td>
<td>0.15</td>
<td>0.17</td>
</tr>
<tr>
<td>Direct solar radiation (DIRECTSR)</td>
<td>-0.24</td>
<td>-0.27</td>
</tr>
</tbody>
</table>
Figure 2.1. Ordination diagram of NMDS axes one and two. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = *Ambrosia dumosa*; atrcon = *Atriplex confertifolia*; atrpol = *Atriplex polycarpa*; cylech = *Cylindropuntia echinocarpa*; encvir = *Encelia virginensis*; ephnve = *Ephedra nevadensis*; ephtor = *Ephedra torreyana*; gutpp = *Gutierrezia species*; hymsal = *Hymenoclea salsola*; kraere = *Krameria erecta*; latri = *Larrea tridentata*; lycand = *Lycium andersonii*; menspi = *Menodora spinescens*; opubas = *Opuntia basilaris*; psotre = *Psorothamnus fremontii*; xyltor = *Xylorhiza tortifolia*; yucsch = *Yucca schidigera*
Figure 2.2. Ordination diagram of NMDS axes one and three. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = *Ambrosia dumosa*; atrcon = *Atriplex confertifolia*; atrpol = *Atriplex polycarpa*; cylech = *Cylindropuntia echinocarpa*; encvir = *Encelia virginensis*; ephnve = *Ephedra nevadensis*; ephtor = *Ephedra torreyana*; gutspp = Gutierrezia species; hymsal = *Hymenoclea salsola*; kraere = *Krameria erecta*; latri = *Larrea tridentata*; lycand = *Lycium andersonii*; menspi = *Menodora spinescens*; opubas = *Opuntia basilaris*; psofre = *Psorothamnus fremontii*; xyltor = *Xylorhiza tortifolia*; yucsch = *Yucca schidigera*. 
Figure 2.3. Ordination diagram of NMDS axes two and three. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = Ambrosia dumosa; atrcon = Atriplex confertifolia; atrpol = Atriplex polycarpa; cylech = Cylindropuntia echinocarpa; encvir = Encelia virginensis; ephnev = Ephedra nevadensis; ephtor = Ephedra torreyana; gutspp = Gutierrezia species; hymsal = Hymenoclea salsola; kraere = Krameria erecta; latri = Larrea tridentata; lycand = Lycium andersonii; menspi = Menodora spinescens; opubas = Opuntia basilaris; psorfrem = Psorothamnus fremontii; xyltor = Xylorhiza tortifolia; yucsch = Yucca schidigera
Figure 2.4. CCA ordination diagram. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = *Ambrosia dumosa*; atrcon = *Atriplex confertifolia*; atpol = *Atriplex polycarpa*; cylech = *Cylindropuntia echinocarpa*; encvir = *Encelia virginensis*; ephne = *Ephedra nevadensis*; ephtor = *Ephedra torreyana*; gutspp = *Gutierrezia species*; hymsal = *Hymenoclea salsola*; kraere = *Krameria erecta*; latri = *Larrea tridentata*; lycand = *Lycium andersonii*; menspi = *Menodora spinescens*; opubas = *Opuntia basilaris*; psofre = *Psorothamnus fremontii*; xyltor = *Xylorhiza tortifolia*; yucsch = *Yucca schidigera*
CHAPTER 3

ABIOTIC INFLUENCE ON COMPETITION AND FACILITATION ON A MOJAVE DESERT BAJADA: A SPATIAL PATTERN ANALYSIS

Abstract. Despite years of debate concerning the roles of competition and facilitation in structuring arid plant communities, the answers are still not apparent. Plant dispersion patterns are often used as indicators of the occurrence either competitive or facilitative interactions. This study examined spatial point patterns of woody perennial species growing on a Mojave Desert bajada in an effort to gain insights into the plant-plant interactions shaping the resident communities. Special focus was given to the possible roles of soil and geologic substrate in shaping community spatial characteristics. In order to accurately assess dispersion patterns, we utilized two different statistical techniques, the more traditional Morisita’s index of dispersion, and a relatively novel approach employing Ripley’s K-function to analyze precise spatial data. Results from both methods indicate that random and clumping patterns are the predominant plant spatial patterns on this site and patterns changed between soils and geologic substrates of different textures and ages. These results demonstrate the strong influence of substrate in shaping plant-plant interactions in arid environments. They also support previous research citing facilitation as an important process driving arid plant community structure.
INTRODUCTION

Ecologists have long debated the roles of competition and facilitation in structuring ecological communities. Nowhere is this debate more apparent than in arid plant communities. Given that water is the principal limiting factor in desert ecosystems, classic theory predicts that plants must compete with neighbors for its uptake. More recently, the stress gradient hypothesis postulates that facilitative, rather than competitive, interactions may be more prevalent in harsh environments whereby neighbors ameliorate abiotic stress (Bertness and Callaway 1994, Stachowicz 2001, Bruno et al. 2003, Armas & Pugnaire 2005, Brooker et al. 2008, Malkinson and Tielbörger 2010).

Plant dispersion patterns have often served as indicators of the ecological processes that may have shaped community structure (Fowler 1986, Legendre and Fortin 1989, Andersen 1992, Legendre 1993, Haase 1995, Schenk et al. 2003, Rayburn et al. 2011). The spatial point pattern or dispersion of individuals in a population describes their spacing relative to each other. There are a wide variety of methods available to test for spatial pattern, many of which are based on the model of complete spatial randomness (CSR). The null hypothesis under this model is that points (plants) occur independently of one another in a random pattern. One alternative to this model is clumped (also referred to as aggregated, underdispersed, or contagious) dispersion, which indicates that the presence of one point increases the probability of finding another in its vicinity. The other alternative is the uniform (also referred to as regular or overdispersed) pattern,
which indicates that a point’s presence reduces the probability of finding another nearby (Pielou 1960, Bailey and Gatrell 1995, Dale 1999, Marcon 2012).

The departures from the null model of CSR are what ecologists use to make inferences about community forming processes. In desert perennial communities, clumped patterns have been attributed to plant-plant facilitation, heterogeneity of soil resources, limited seed dispersal, or vegetative reproduction (Bertness and Callaway 1994, Schlesinger et al. 1996, Schlesinger and Pilmanis 1998, Walker et al. 2001, Titus et al. 2002, Brooker et al. 2008), whereas uniform patterns have been associated with plant-plant competition for limited resources leading to density-dependent mortality (Ebert and McMaster 1981, MacMahon and Schimpf 1981, Philips and MacMahon 1981, Prentice and Werger 1985, Perry et al. 2002, Schenk et al. 2003, Perry et al. 2009). Fowler (1986) explained that the variable climates of deserts tend to produce fluctuating resource levels, which, at times, may cause the size of populations to decrease below the level at which competition would occur. However, if a series of “good” years where resource availability and the carrying capacity of the environment increases, is followed by a “bad” year where resource levels drop, competition for resources becomes intense. Competition should convert clumped distributions into random ones, and random distributions into uniform ones, with uniform distributions originating during long droughts. Based on this hypothesis, smaller plants should show more clumped patterns while larger individuals should tend toward uniformity (Philips and MacMahon 1981, Cody 1986, Skarpe 1991, Haase et al. 1996).
Drought induced perennial plant mortality may be one of the most important processes affecting plant community structure in deserts and drought response tends to be soil specific (Hamerlynck and McAuliffe 2008, McAuliffe and Hamerlynck 2010). Soil texture, age, and horizon development dictate water availability. Subtle differences in soil properties may lead to large differences in the amount of water that can be stored and absorbed (Yang and Lowe 1956, MacMahon and Wagner 1985, Hamerlynck et al. 2000, Hamerlynck et al. 2002, Hamerlynck et al. 2004, McAuliffe et al. 2007, Ignace and Huxman 2009, Webb 2009, Schwinning et al. 2011). Soil hydrologic properties thus direct the distribution and pattern of plant communities.

The phenomenon of soil particle sorting on bajada gradients and its influence on plant communities has been well established (Philips and MacMahon 1978, MacMahon and Schimpf 1981, MacMahon and Wagner 1985, Bowers and Lowe 1986). This model works as a generalization; smooth gradients such as this rarely exist (Parker 1995). The classic bajada gradient model oversimplifies the complexities of specific soil and geologic (i.e. parent material) types. Several studies have investigated water relations and growth patterns between soil types (Smith et al. 1995, Hamerlynck et al. 2000, Hamerlynck et al. 2002), but to our knowledge, only one that has looked at the influence of soil type on dispersion patterns. Schenk et al. (2003) examined the spatial pattern of a single species, *A. dumosa*, on two different geologic substrates. They found that subtle differences in substrate were correlated with differences in the spatial distribution of *A. dumosa* plants.
This study will investigate the dispersion patterns within and among plant communities across a Mojave Desert bajada. Species spatial patterns will be examined between plant communities on different soil and geologic substrates. We will give special focus to the dominant shrubs, *L. tridentata* and *A. dumosa* which cover approximately 70% of the Mojave Desert (MacMahon 2000, Rundel and Gibson 1996). Given the large role of soil properties in structuring desert plant communities, we expect that changes in plant dispersion patterns will coincide with changes in soil and geologic types. Specifically, we expect to see dispersion patterns shift from clumped to uniform as environmental stress increases.

Historically, clumped and random patterns are detected more often in the desert southwest, but there have been a few reported cases of uniformity in *L. tridentata* (Barbour 1969, Woodell et al. 1969, Fonteyn and Mahall 1981, Philips and MacMahon 1981, Schlesinger and Jones 1984). These occurrences are often challenged on the premise of methodological and statistical inadequacies (Anderson 1971, Barbour 1973, King and Woodell 1973, Ebert and McMaster 1981, King and Woodell 1984, Prentice and Werger 1985, Fowler 1986, King and Woodell 1987, Cox 1987). In particular, spatial pattern is scale dependent and results vary based on plot size and plant density. In addition, *L. tridentata*, the most prominent warm desert shrub, is difficult to count as individual shrubs due to its clonal growth patterns (Ebert and McMaster 1981, King and Woodell 1984, Schlesinger and Jones 1984, Fowler 1986). In addition to methodological difficulties, care must be taken in inferring causation given the many different processes that may generate the same spatial patterns (Perry et al. 2002, Escudero et al. 2005). It is
likely that spatial patterns are the product of multiple interacting processes that change based on the age or life history of individuals (Schenk et al. 2003, Escudero et al. 2005, Miriti 2006). Current research efforts are focusing more on how competition and facilitation balance in harsh environments (Schenk and Mahall 2002, Escudero et al. 2005, Armas & Pugnaire 2005, Miriti 2007).

In order to accurately assess dispersion patterns, we will utilize two different statistical techniques and compare the results. The first, Morisita’s index of dispersion, will be used on a broad scale dataset composed of species count data. The second technique is a relatively novel approach that employs Ripley’s K-function to analyze precise spatial data in order to determine dispersion patterns (Rayburn et al. 2011). By using two different techniques, we aim to eliminate sources of bias imposed by only using one statistical method. With reliable results, we hope to shed some light on the long held controversy between competition and facilitation in arid plant communities.

METHODS

Study area

The Upper Las Vegas Wash Conservation Transfer Area (ULVWCTA), Nevada, consists of a 7,400 ha land parcel of Mojave Desert vegetation on alluvial fan (bajada) and basin floor deposits derived from the Spring and Sheep Mountains. The area sits north of Las Vegas and is transected by a complex of Pleistocene spring deposits and their attendant washes. A research team from Utah State University was tasked with creating vegetation and soils maps of the ULVWCTA. This effort identified seven
vegetation associations and eight soil types across the site (MacMahon et al. 2008). These maps, in addition to geologic data obtained from a USGS map (1:100,000 Geologic and Geophysical maps of the Las Vegas 30’ X 60’ Quadrangle, Clark and Nye Counties, Nevada, and Inyo County, California (Page et al. 2005), were used in the spatial analyses. Tables 3.1, 3.2, and 3.3 provide lists and descriptions of each vegetation association, soil type, and geologic unit respectively.

Vegetation sampling and analyses

Mapping dataset. The vegetation data collected for the MacMahon et al. (2008) mapping effort was used as the first dataset for spatial analysis. A stratified sampling design provided a total of 240 plots sampled across the ULVWCTA. Two strata, based on broad geomorphic categories, were identified. The first was defined as alluvial fan/wash and totaled 5,270 ha (71%) of the ULVWCTA. The second stratum (2,130 ha, 29%) was defined as basin floor/spring deposit, and was associated with past groundwater discharge (evidenced by highly calcareous spring deposits) and lacustrine sediments.

A total of 240 plots were sampled across the ULVWCTA. Initially, the mapping data consisted of 163 sample plots that were systematically distributed along 13 north-south transects spaced 2000 meters apart. Vegetation data were collected every 100 meters in the basin floor/spring deposit stratum and every 500 meters in the alluvial fan/wash stratum. Preliminary evaluation of these data indicated inadequate coverage of the area, so an additional 77 sample plots were established and surveyed to increase sampling intensity where vegetation variation was greater, and where spectral reflectance
data from Landsat 7 and ASTER satellites suggested greater complexity in geomorphic surfaces and vegetation.

Each sample plot consisted of the area of a circle with a 10-m radius. Each circular plot was divided into quarters by an east-west and a north-south line. One quarter of each plot was used to survey vegetation. The quarter chosen for sampling was rotated in a clockwise manner from one sample plot to the next. Vegetation data were collected for woody perennials only. For each plant within the sample quarter, the height, width in two directions (the longest width and the width perpendicular to this), and species were recorded.

Plant spatial patterns for this dataset were assessed using Morisita’s index of dispersion, a quadrat based method (Hurlbert 1990, Bailey and Gatrell 1995, Dale 1999, Dale et al. 2002, Perry et al. 2002). This method uses counts of plants in quadrats in order to determine random, clumped, or uniform dispersion patterns. Morisita’s Index of Dispersion was designed to remove the effect of quadrat size on the measure of aggregation. Morisita’s Index of Dispersion can be defined as (Morisita 1959, Krebs 1999):

$$I_d = n \frac{\sum x^2 - \sum x}{(\sum x)^2 - \sum x}$$

Where $I_d$ = Morisita’s index of dispersion

$n$ = sample size

$\sum x$ = Sum of the quadrat counts = $x_1 + x_2 + x_3 \ldots$
\[ \sum x^2 = \text{sum of quadrat counts squared} = x_1^2 + x_2^2 + x_3^2 \]

\( I_d \) values range from 0 to \( n \). \( I_d = 1 \) for random patterns. Uniform patterns fall between 0 and 1 and clumped patterns fall between 1 and \( n \).

Morisita’s Index can be standardized on a scale of -1 to +1. To calculate the standardized Morisita index \( (I_p) \), the Morisita's index of dispersion \( (I_d) \) and two critical values, the uniform index \( (M_u) \) and the clumped index \( (M_c) \) are calculated first:

Uniform index =

\[
M_u = \frac{\chi_{975}^2 - n + \sum x_i}{(\sum x_i) - 1}
\]

Clumped Index =

\[
M_c = \frac{\chi_{025}^2 - n + \sum x_i}{(\sum x_i) - 1}
\]

where \( \chi_{975}^2 \) and \( \chi_{025}^2 \) are the values of the chi-squared with \((n-1)\) degrees of freedom that have 97.5% or 2.5% of the area to the right, \( n \) is the number of quadrats, and \( x_i \) is the number of plants in quadrat \( i \) \( (i = 1, \ldots, n) \). The \( I_p \) is then calculated by one of the four following formulas:
when \( I_d \geq M_c > 1.0 \):

\[
I_p = 0.5 + 0.5 \left( \frac{I_d - M_c}{n - M_c} \right)
\]

when \( M_c > I_d \geq 1.0 \):

\[
I_p = 0.5 \left( \frac{I_d - 1}{M_c - 1} \right)
\]

when \( 1.0 > I_d > M_u \):

\[
I_p = -0.5 \left( \frac{I_d - 1}{M_u - 1} \right)
\]

when \( 1.0 > M_u > I_d \):

\[
I_p = -0.5 + 0.5 \left( \frac{I_d - M_u}{M_u} \right)
\]

The standardized Morisita index \( (I_p) \) is independent of sample size and population density and ranges from -1 to +1, with 95% confidence limits at +0.5 and -0.5. For random patterns, \( I_p \) equals zero, clumped patterns above zero, and uniform patterns below zero (Krebs 1989). Analyses were conducted using the Vegan package (version 2.0-0, Oksanen et al. 2011) for R (version 2.13.2; R Development Core Team, Vienna, Austria 2011).

**Transect dataset.** In addition to the broad scale mapping dataset, two additional transects were surveyed in order to observe species spatial patterns at a finer scale with more precise spatial data. The first transect consisted of 13, 20 x 20 m plots. Plots were established every 300 meters as well as where known vegetation, soil, or geologic changes occurred. These changes were assessed by overlaying vegetation, soil, and
geology maps within a GIS system. Plots were placed within the boundaries of known vegetation, soil, and geologic units. If a plot happened to fall in an area that was heavily dissected, a suitable homogenous site was located in the near vicinity. This transect was 3862 m long and ranged between 791 m - 865 m elevation. It crossed five different geologic types, three soil types, and three vegetation associations and was designed to capture differences that may exist between soil, geology, and vegetation types.

The second transect was constrained to the upper bajada in the *Larrea tridentata - Ambrosia dumosa* association. This association is characterized by areas where *L. tridentata* and *A. dumosa* comprise ≥70% of the relative plant density. Soil type and geologic type did not change within this transect. It consisted of 10, 20 x 20 m plots, was 3058 m long, and ranged from 835 m – 870 m elevation. This transect was designed to see if spatial patterns changed with mild elevation changes.

Within each 20 x 20 m plot, plant dimensions of woody species only were measured as described for the mapping dataset. In addition, plant locations (UTM coordinates) were measured using a ProMark™ 3 survey grade GPS unit. Locations were post-processed using GNSS Solutions software (v.3.10.01, Magellan Navigation 2007) with the resulting point locations being within three centimeters from actual plant center (Rayburn et al. 2011).

The UTM coordinates from the transect datasets were analyzed using Ripley’s K-function, a second-order statistic (Dale 1999). Second-order statistics are based on the distribution of pairs of points. Ripley’s K-function uses information on all inter-point distances over a range of distance scales (t), therefore it is able to detect mixed patterns at
different scales (Weigand and Maloney 2004). It is a cumulative test and allows inferences to be made at specific distances (Perry et al. 2006). Ripley’s K-function can be defined as (Andersen 1992, Haase 1995, Schiffer et al. 2008):

\[
\hat{R}(t) = n^2A \sum \sum w_{ij}^{-1} I_t(u_{ij})
\]

Where,  
\( n \) = the number of events (plants) in the study plot  
\( A \) = area of the plot  
\( I_t \) = a counter variable, if \( u_{ij} < t \) then \( I_t = 1 \), otherwise zero  
\( u_{ij} \) = the distance between events \( i \) and \( j \)  
\( w_{ij} \) = a weighting factor to correct for edge effects  
\( t \) = a given range of distances


\[
\hat{L}(t) = \sqrt{\hat{R}(t)/\pi}
\]

The L-function was plotted as (\( \hat{L}(t) - t \)) against \( t \). Under the null hypothesis of CSR, the transformation has an expected value of 0 for all values of \( t \). Monte Carlo permutations (\( N_{sim} = 199 \)) were used to produce a 95% confidence intervals for \( \hat{L}(t) \) to test the departure of the pattern from CSR. Rejection limits are estimated as simulation
envelopes (Haase 1995, Perry et al. 2006). Positive values above the upper confidence envelope indicate a clumped distribution and negative values below the confidence envelope indicate uniform pattern. Values within the confidence envelope indicate random pattern. Analyses were performed using the Spatstat package (version 1.24-2, Baddeley & Turner 2005) for R (version 2.13.2; R Development Core Team, Vienna, Austria 2011). For comparison, the transect dataset was also analyzed using Morisita’s Index of Dispersion.

RESULTS

*Mapping dataset, Morisita’s index of dispersion*

A total of 6,759 individual plants were identified and measured within the 240 mapping plots. Appendix A provides a list of all species that were identified during field work on the ULVWCTA. Appendix B provides a list of all the mapping plots with corresponding elevation, vegetation associations, soil types, and geologic units. Appendix C provides a list and frequency count for all species identified in the mapping plots.

Morisita’s Index of Dispersion was used to distinguish dispersion patterns for woody perennials measured in the mapping dataset. Analyses were run for all plots together, by soil type, vegetation association, geologic unit, and by size class. Species that occurred in less than ten plots overall were not included in the analyses. Size classes were based on cover, with cover calculated as the area of an ellipse (long width x width perpendicular to the long width x \( \pi \)). The size classes were <100 cm\(^2\), 100-1,000 cm\(^2\),
1,000-10^4 cm^2, 10^4-10^5 cm^2, and >10^5 cm^2. In some cases, common species were absent or occurred in only one plot in some soil types, vegetation associations, geologic units, or size classes. In these cases, the statistical software did not run the analysis and “NA” was entered in the results table for the respective species. Both the Morisita’s Index of dispersion (I_d) and the standardized Morisita Index (I_p) are reported. Results for all plots together and by size class are reported in Table 3.4, results by soil type are in Table 3.5, results by vegetation association are in Table 3.6, and results by geologic unit are in Table 3.7.

Every species exhibited a clumped pattern when all plots were examined together. Most species displayed a clumped pattern within soil, vegetation, geology, and size class subsets. There were 22 cases that deviated from a clumped pattern, all of which were uniform in pattern. After close inspection, 19 of these cases appear to be an artifact of small sample sizes in which there were only a few individuals in the given sample subset and all of these individuals occurred in separate plots. These cases of deviation from random pattern are likely unreliable and marked with an asterisk in the results tables. The three remaining instances of uniform pattern had larger sample sizes and involved L. tridentata. One of these cases occurred in the largest size class, one occurred in the Ambrosia dumosa - Larrea tridentata: Upper Alluvial Fan Association, and one occurred in the Qfy geologic unit.

*Transect dataset, L-function analyses*

A total of 2,348 plants were measured and mapped with the ProMark™ 3 GPS unit in the 23 transect plots. Appendix G provides a list of all the transect plots with corresponding elevation, vegetation associations, soil types, and geologic units.
Appendix H provides a list and frequency count for all species identified in the transect plots.

Three different L-function analyses were run for each plot. The first included all species together. If sample size permitted, additional analyses were run for A. dumosa alone and L. tridentata alone. All results have been summarized in Table 3.8 (Transect 1) and Table 3.9 (Transect 2). Results were interpreted from plots of \( \hat{L}(t) - t \) against \( t \) with a 95% confidence envelope. These plots are provided in Appendix I.

**Transect 1.** When observing all species together, all plots showed a random pattern for either all or some of the observed spatial scales \( t \). Plots 4, 5, 12, and 13 showed significant clumping at distances greater than 0.5. Plots 3, 9, and 10 showed significant clumping at smaller distances \( t \approx 0.5 - 1.5 \). In addition, plot 9 showed significant clumping when \( t \approx 4.0 - 5.5 \).

When A. dumosa was analyzed alone, plots 10, 12, and 13 showed significant clumping at distances greater than \( t \approx 0.6 - 1.0 \). Plots 1, 3, 6, and 9 showed finer scale to intermediate clumping \( t \approx 0.6 - 4.0 \). L. tridentata showed significant clumping in four plots at intermediate to larger distances \( t \approx 1.3 - 6 \).

**Transect 2.** When observing all species together, all plots showed a random pattern for either all or some of the observed spatial scales \( t \). Plots 1, 4, and 8 showed significant clumping at smaller distances \( t \approx 0.5 - 1.5 \) while plots 4 and 8 showed additional clumping at intermediate distances \( t \approx 2.4 - 4.9 \). Looking at A. dumosa alone, plots 3, 4, 5, 6, and 8 showed significant clumping at smaller scales \( t \approx 0.5 - 3.3 \).
and plot 6 showed significant clumping when $t > 3.0$. *L. tridentata* displayed a random pattern at all scales.

**Transect dataset, Morisita’s Index of Dispersion**

Morisita’s Index of Dispersion was used to distinguish dispersion patterns for woody perennials measured in the transect dataset. Analyses were run for all plots together and by size class. In some cases, species were absent or occurred in only one plot in some size classes. In these cases, the statistical software did not run the analysis and “NA” was entered in the results table for the respective species. Results are reported in Table 3.10. Both the Morisita’s Index of dispersion ($I_d$) and the standardized Morisita Index ($I_p$) are reported.

Most species displayed a clumped pattern. There were six cases that deviated from a clumped pattern, all of which appear to be an artifact of small sample sizes where there were only a few individuals in the given sample subset and all of these individuals occurred in separate plots. These cases of deviation from random pattern are likely unreliable and marked with an asterisk in the results table.

**DISCUSSION**

The objective of this study was to identify the spatial patterns of woody perennial species growing on the ULWVCTA and compare the patterns between plant communities, soil types, geologic types, and plant size categories. Results from both the mapping and transect datasets analyzed with Morisita’s Index of Dispersion and the transect dataset analyzed with the L-function indicate that random and clumping patterns
are the dominant plant spatial patterns across the ULVWCTA. However, Morisita’s Index of Dispersion reported a majority of patterns as clumped with only three uniform patterns while the L-function reported a majority of patterns as random with some clumping at certain spatial scales. The L-function didn’t report any uniform patterns. These differences are likely due to mathematical and scale differences between the two statistical techniques. Results from each dataset are discussed in detail below.

Mapping dataset, Morisita’s index of dispersion

There were three instances of uniform pattern identified in mapping dataset analyzed with Morisita’s index of dispersion. The rest were clumped. All three instances of uniform pattern involved *L. tridentata* and are discussed in the following paragraphs.

In the mapping dataset, *L. tridentata* changes from clumped in all of the smaller size classes to uniform in the largest. This pattern supports earlier observations that there is a positive correlation between plant size and distance between plants (Philips and MacMahon 1981, Fowler 1986). There were ten plots with *L. tridentata* in the largest size class. Of these plots, eight have younger, Holocene aged, alluvial fan/wash geology (Qay Qayy, or Qfy). The soils in these areas are weakly developed and composed of coarse soil particles. *L. tridentata* has likely reached large sizes on these sites due to extra water availability from channel activity in addition to water seepage into the coarse, weakly developed soils. Previous research supports the pattern of *L. tridentata* growing larger on younger soils (McAuliffe 1994, Hamerlynck et al. 2002, McAuliffe et al. 2007). The larger *L. tridentata* have probably experienced a series of resource pulses with a
corresponding fluctuation in carrying capacity. Resource competition during drought periods may have produced the uniform distribution through density dependent mortality.

The other two plots with large uniform *L. tridentata* occurred on basin floor/spring deposit soils with geologic unit Qscd. These are older, lower elevation sites of the Late Pleistocene, composed of fine-grained soils of light-gray calcareous mud associated with past ground water discharge. Water availability is typically low on these soils which may have led to competition among plants for available moisture. Evidence of this is seen in the low plant diversity and density on these sites. Large *L. tridentata* plants exist as some of the only vegetation in the area and likely used much of the available water resources.

*L. tridentata* exhibits another uniform pattern in the *Ambrosia dumosa - Larrea tridentata*: Upper Alluvial Fan Association. There were nine plots sampled in this association and all nine had uniform distribution of *L. tridentata*. There were 22 *L. tridentata* plants throughout the nine plots, ranging from one to five plants per plot. This association has the highest mean elevation of all the associations and occurs on the Weiser-Wechech soil association and Qayo geologic unit (an “older” young alluvium of the Holocene and latest Pleistocene). The Weiser-Wechech soil is characterized by an accumulation of calcium carbonate as coatings and a trace of secondary silica on the bottoms of rock fragments in the subsoil with the possibility of a petrocalcic horizon which may limit plant available moisture. Overall plant density was low and six of the nine plots contained *A. confertifolia* and/or *Psorothamnus fremontii*. *A. confertifolia* and *P. fremonttii* are often associated with gypsiferous soils in the Mojave (Meyer 1986) and
the soils in this association are suspected to have a higher alkalinity than the surrounding alluvial fan areas (MacMahon et al. 2008). Soil texture and chemistry and possible petrocalcic horizons have likely limited water availability on these sites thus promoting the uniform pattern of *L. tridentata* through competition.

*L. tridentata* also presented a uniform pattern in the geologic unit Qfy. Qfy is a younger, intermittently active, fine grain alluvial deposit with sand, silt, mud, and interbedded gravel. There were only four plots sampled in the Qfy unit, three of which occurred on the Dalian-McCullough soil complex and one on Las Vegas-DeStazo complex. The Dalian-McCullough complex is a very gravelly fine sandy loam occurring on fan skirts which transition to lower elevation alluvial flats and the Las Vegas-DeStazo complex is a gravelly sandy loam occurring on alluvial flats. Vegetation in these plots was sparse, consisting primarily of *A. dumosa* and/or *L. tridentata*. This is another example of fine grained soils limiting plant available moisture, a possible explanation for the uniform pattern observed in *L. tridentata*.

**Transect dataset, L-Function analyses**

*Transect 1.* Spatial patterns in Transect 1 appear to change as soil type, geologic unit, and vegetation association change down the bajada (Plots 1-5), across a wash (Plot 6) and badland area (Plots 7 and 8), and rise again onto another fan (Plots 9-13). Plots 1-5 occur on the Weiser-Wechech soil association. Plots 1 and 2 are in the Qay geologic unit and the *Larrea tridentata - Ambrosia dumosa* vegetation association while plots 3, 4, and 5 are in the Qayo geologic unit and *Ambrosia dumosa - Larrea tridentata: Upper Alluvial Fan* vegetation association. Plots 1 and 2 show random plant patterns across all species combined and some clumping at intermediate distances for both *A. dumosa* alone
(only Plot 1) and L. tridentata alone (only Plot 2). More clumping patterns appear as the vegetation and geology change in Plots 3, 4, and 5. Plot 3 shows some clumping at small scales across all species while Plots 4 and 5 show more clumping at all scales across all species. The clumping patterns persist when observing A. dumosa and L. tridentata alone although there weren’t enough A. dumosa individuals in Plots 4 and 5 to analyze this species individually. Plots 4 and 5 are sparse with desert pavement covering most of the plot area. The patterns for L. tridentata on plots 3, 4, and 5 contradict those from the mapping dataset on the Qayo geologic unit and Ambrosia dumosa - Larrea tridentata: Upper Alluvial Fan vegetation association where we observed uniform patterns. It is possible that the prevalence of desert pavement on plots 4 and 5 has forced the plants into clumping patterns.

Plot 6 is in the Larrea tridentata - Ambrosia dumosa vegetation association but sits within the Dalian-McCullough soil complex and Qayy geologic unit. This is a younger alluvial fan site with intermittently active washes. This plot shows random pattern across all species and for L. tridentata alone. A. dumosa shows some clumping at intermediate distances. Plots 7 and 8 are in the Badland soil type, L. tridentata vegetation association, with geologic unit Qscd. These are spring deposit areas typified by light-gray calcareous soils with sparse vegetation. This is one of the most stressful habitats in the ULVWCTA as evidenced by the scant plant cover. Dispersion patterns were random across all species and for L. tridentata alone. There weren’t enough A. dumosa individuals to analyze individually. The prevalence of random patterns and lack of clumping patterns could be indicative of a trend towards competitive uniform patterns.
Plots 9-13 increase in elevation (after Plot 8) and are all within the Weiser-Wechech soil association, *Larrea tridentata - Ambrosia dumosa* vegetation association, and have either Qay or Qayo geology. Plots 9, 10, 12, and 13 show some clumping for all species together and for *A. dumosa* alone. *L. tridentata* has an entirely random pattern for all plots except Plot 13 where it shows clumping at larger scales. Plot 13 is sparse and a majority of the plot is covered by desert pavement. Again, the clumping patterns are possibly due to habitat heterogeneity from desert pavement sites. Plot 11 shows random patterns for all analyses.

**Transect 2.** Transect 2 was designed to keep soil type, geologic unit, and vegetation association constant in order to observe pattern changes that may occur with subtle elevation changes. All plots in Transect 2 were in the Weiser-Wechech soil association, the Qay geologic unit, and the *Larrea tridentata - Ambrosia dumosa* vegetation association. Overall, there were some clumping patterns for all species together (Plots 1, 4, and 8) and for *A. dumosa* alone (Plots 3-6 and 8). *L. tridentata* exhibited random patterns in all plots. Clumping patterns for *A. dumosa* alone occurred at smaller scales similar to the pattern observed in Transect 1. There didn’t appear to be any pattern changes associated with the elevation change in this transect.

While the results from the two datasets and analytical techniques differ, they still support previous findings that clumped and random patterns are more common than uniform patterns in desert plant species (Barbour 1969, Woodell et al. 1969, Barbour and Diaz 1973, Philips and MacMahon 1981, Schlesinger and Jones 1984, Cody 1986, Fowler 1986, Manning and Barbour 1988, Smith 1997, Eccles et al. 1999, Rayburn et al.
The patterns we observed for *L. tridentata* and *A. dumosa* were also similar to those observed in previous work. Namely, we saw a prevalence of clumped patterns for *A. dumosa* (Fonteyn and Mahall 1981, Schlesinger and Jones 1984, Miriti 2006) and some evidence of the clumped to random to uniform pattern progression with increasing plant size in *L. tridentata*. It has been proposed that in order for regular patterns to develop, a species must be long lived and have episodic seedling establishment generating even aged stands (Barbour 1973, Fonteyn and Mahall 1981), both of which have been observed in *L. tridentata* (Barbour 1969, Mabry et al. 1977). *L. tridentata* is an exceptionally drought hardy, long lived species, some of which have been established in the Mojave Desert for thousands of years (Mabry et al. 1977, Vasek 1980, Koehler et al. 2005), possibly long enough to develop uniform patterns. *A. dumosa* is a shorter lived, drought deciduous, natural colonizer where individuals may not survive long droughts to develop uniform patterns. When looking at decade scale severe drought, McAuliffe and Hamerlynck (2010) saw greater *A. dumosa* mortality as opposed to *L. tridentata*.

This study also shows a predominance of clumping patterns occurring at smaller scales. This supports models showing that the roles of facilitation and competition are influenced by lifestage (Callaway 1995, Callaway and Walker 1997, Miriti 2006). Seedlings are often found spatially aggregated with adult nurse plants which improve the harshness of the environment (Padien and Lajtha 1992, McAuliffe 1984, McAuliffe 1988, Callaway and Walker 1997, Toft and Fraizer 2003, Miriti 2006, Kéfi et al. 2008). As the
seedlings grow, they often become competitors of the nurse plant, as seen in widespread nurse plant mortality (McAuliffe 1988, Callaway and Walker 1997).

While statistics are capable of labeling patterns, we are still left hypothesizing what processes generate the patterns. Based on the frequency of clumped and random patterns, we could conclude that this study supports theories claiming that net positive interactions are a dominant force in harsh environments. However, the observed clumping may be result a of habitat heterogeneity, not necessarily facilitative interactions. Given that arid ecosystems are naturally heterogeneous and nurse plants are a common feature, future research should look to unravel the relative role of each of these in generating the clumped patterns of desert perennials.

Regardless of the abundance of clumped and random patterns and the paucity of uniform patterns, we can’t conclude that competition isn’t an important process in arid plant communities. Barbour (1973), and Philips and MacMahon (1981) emphasize that uniform patterns are rare and unlikely to form given the heterogeneous nature of arid environments. In addition, periodic drought may force plants back into clumped patterns before uniform patterns have time to develop. Given that we only see uniform patterns in the long lived L. tridentata, we conclude that it takes a tremendous amount of time for uniform patterns to develop. The prevalence of random patterns in L. tridentata identified by the L-function may be a reflection of a changing community, one that has not aged enough to form uniform patterns. On the other hand, it may also be direct result of habitat heterogeneity. If patterns really do change from clumped to random to uniform under increasing competitive pressure, then these plants should be experiencing
competitive interactions once one plant in a clump grows large enough to consume resources needed by neighbors.

If we continue to use the uniform pattern as an indication of competition, more long term studies need to examine how long uniform patterns take to emerge. We may be looking for evidence that can never be observed in our lifetime. We also suggest examining pattern at smaller scales, at the site of nurse plants and individual islands of fertility. Miriti (2006) notes that seedling location under an adult canopy may enhance growth but that overcrowding from other juveniles may reduce survival and outweigh facilitative benefits. Perhaps uniform patterns may exist within a small clump or island. Interestingly, though not statistically significant, the L-function plots from the transect datasets show small scale dispersion patterns (<0.5 meters) dipping towards uniform in all but two plots (Appendix I).

Despite years of debate concerning the roles of competition and facilitation in structuring arid plant communities (Goldberg and Novoplansky 1997, Chesson et al. 2004, Maestre et al. 2009), the answers are still not apparent. Clearly, competitive and facilitative interactions may fluctuate or act simultaneously in complex ways (Callaway 1995, Schenk and Mahall 2002, Butterfield et al. 2010). We have seen evidence of multiple working hypotheses including the stress gradient hypothesis, competition for limited water, and ontogenetic shift between facilitation and competition. Future research should focus on the interchange between positive and negative interactions and how plant age, size, and density might affect these relationships.
On the whole, our results exemplify the influence of soil and geologic properties in shaping plant dispersion patterns in arid ecosystems. As predicted, we saw plant dispersion patterns shift from clumping to random to uniform as environmental stress increased. With the exception of large *L. tridentata* growing on geologic units Qay Qayy, and Qfy, our data show dispersion patterns tending toward random or uniformity on older finer soils with more horizon development where moisture is not readily accessible. We suggest that habitat heterogeneity plays a larger role in determining plant spatial patterns than either competition or facilitation. As such, soil, geology, and parent material should always be considered when designing prospective research on arid plant communities. Understanding the relationship among these abiotic factors and plant-plant interactions is essential in making careful conservation and management decisions for desert ecosystems.

ACKNOWLEDGMENTS

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LITERATURE CITED


Table 3.1. Vegetation associations of the ULVWCTA.

<table>
<thead>
<tr>
<th>Vegetation Association</th>
<th>Description</th>
<th>Area (ha)</th>
<th>Elevation (m)</th>
<th>Number of plots sampled</th>
<th>Richness</th>
<th>Density (n/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Larrea tridentata</em> - <em>Ambrosia dumosa</em> Association</td>
<td><em>Larrea tridentata</em> and <em>Ambrosia dumosa</em> compose ≥70% of the relative density</td>
<td>5,817</td>
<td>659 to 929</td>
<td>143</td>
<td>34</td>
<td>3889</td>
</tr>
<tr>
<td><em>Larrea tridentata</em> Association</td>
<td><em>Larrea tridentata</em> is the dominant shrub and these areas coincide with basin floor soils</td>
<td>286</td>
<td>729 to 828</td>
<td>11</td>
<td>7</td>
<td>463</td>
</tr>
<tr>
<td><em>Atriplex polycarpa</em> - <em>Ambrosia dumosa</em> Association</td>
<td><em>Atriplex polycarpa</em> and <em>Ambrosia dumosa</em> dominate in wet, active, and dry washes</td>
<td>245</td>
<td>658 to 831</td>
<td>19</td>
<td>14</td>
<td>4269</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Menodora spinescens</em> Association</td>
<td><em>Ambrosia dumosa</em> and <em>Menodora spinescens</em> make up the greatest shrub density in the basin floor</td>
<td>42</td>
<td>667 to 715</td>
<td>8</td>
<td>17</td>
<td>9502</td>
</tr>
<tr>
<td>Badlands</td>
<td>barren ground with some <em>Larrea tridentata</em></td>
<td>94</td>
<td>705 to 742</td>
<td>6</td>
<td>4</td>
<td>276</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Larrea tridentata</em>: Upper Alluvial Fan Association</td>
<td><em>Ambrosia dumosa</em> in association with <em>Larrea tridentata</em> make up the greatest density on the upper alluvial fan</td>
<td>36</td>
<td>798 to 876</td>
<td>8</td>
<td>12</td>
<td>2674</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em> - <em>Atriplex confertifolia</em> Association</td>
<td><em>Ambrosia dumosa</em> in association with <em>Atriplex confertifolia</em> characterize this association in the basin floor/spring deposit</td>
<td>445</td>
<td>659 to 724</td>
<td>41</td>
<td>14</td>
<td>2612</td>
</tr>
</tbody>
</table>
Table 3.2: Soil map units of the ULVWCTA.

<table>
<thead>
<tr>
<th>Soil</th>
<th>Parent material</th>
<th>Landform</th>
<th>Drainage class</th>
<th>(Ksat)*</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizo</td>
<td>Mixed alluvium</td>
<td>Channels</td>
<td>Excessively drained</td>
<td>High to very high (5.95 to 19.98 in/hr)</td>
<td>Very gravelly loamy sand</td>
</tr>
<tr>
<td>Dalian-McCullough Complex</td>
<td>Alluvium derived from limestone and dolostone</td>
<td>Fan skirts</td>
<td>Well drained</td>
<td>High (1.98 to 5.95 in/hr)</td>
<td>Very gravelly fine sandy loam</td>
</tr>
<tr>
<td>Las Vegas</td>
<td>Alluvium derived from limestone</td>
<td>Basin-floor remnants</td>
<td>Well drained</td>
<td>Very low (0 in/hr)</td>
<td>Gravelly fine sandy loam</td>
</tr>
<tr>
<td>Las Vegas-DeStazo Complex</td>
<td>Alluvium derived from limestone</td>
<td>Alluvial flats</td>
<td>Well drained</td>
<td>Very low (0 in/hr)</td>
<td>Gravelly fine sandy loam</td>
</tr>
<tr>
<td>Weiser-Wechech Association</td>
<td>Alluvium derived from limestone and dolomite</td>
<td>Fan remnants</td>
<td>Well drained</td>
<td>Moderately high to high (0.57 to 5.95 in/hr)</td>
<td>Extremely gravelly fine sandy loam</td>
</tr>
<tr>
<td>Weiser</td>
<td>Alluvium derived from limestone and dolomite</td>
<td>Fan remnants</td>
<td>Well drained</td>
<td>High (1.98 to 5.95 in/hr)</td>
<td>Extremely gravelly fine sandy loam</td>
</tr>
<tr>
<td>Weiser-Goodyspring Complex</td>
<td>Alluvium derived from limestone and dolomite</td>
<td>Fan remnants</td>
<td>Well drained</td>
<td>High (1.98 to 5.95 in/hr)</td>
<td>Extremely gravelly fine sandy loam</td>
</tr>
<tr>
<td>Badland</td>
<td>Mixed alluvium over lacustrine</td>
<td>Hills on alluvial flats</td>
<td>Well drained</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Ksat=capacity of the most limiting layer to transmit water
Table 3.3: Geologic units of the ULVWCTA.

<table>
<thead>
<tr>
<th>Unit*</th>
<th>Parent Material</th>
<th>Age</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Qai</td>
<td>Intermediate fan alluvium</td>
<td>Late and middle Pleistocene</td>
<td>Cemented alluvial-fan gravel, with interbedded sand; poorly to moderately well sorted</td>
</tr>
<tr>
<td>Qay</td>
<td>Young fan alluvium</td>
<td>Holocene and latest Pleistocene</td>
<td>Noncemented alluvial-fan gravel and sand with weakly developed soil.</td>
</tr>
<tr>
<td>Qayo</td>
<td>Older young alluvium</td>
<td>Holocene and latest Pleistocene</td>
<td>Noncemented gravel and sand with weakly developed soil of alluvial-fan remnants</td>
</tr>
<tr>
<td>Qayy</td>
<td>Youngest alluvium</td>
<td>Holocene</td>
<td>Noncemented alluvial-fan gravel and sand of intermittently active wash complexes</td>
</tr>
<tr>
<td>Qfy</td>
<td>Intermittently active fluvial fine-grained alluvium</td>
<td>Late Holocene</td>
<td>Brown to gray sand, silt, mud, and interbedded gravel.</td>
</tr>
<tr>
<td>Qscd</td>
<td>Intermediate fine-grained deposits associated with past ground-water discharge</td>
<td>Late Pleistocene</td>
<td>Top 1-2 m is characteristically resistant light-gray calcareous mud that is partially cemented with calcite</td>
</tr>
<tr>
<td>Qsu</td>
<td>Undivided young and intermediate fine-grained deposits associated with past ground-water discharge</td>
<td>Early Holocene and late Pleistocene</td>
<td>Light-gray to light-brown unconsolidated silt, sandy silt, silty sand, and mud or the top 1-2 m is characteristically resistant light-gray calcareous mud that is partially cemented with calcite</td>
</tr>
</tbody>
</table>

*Unit= map unit
Table 3.4. Morisita’s index ($I_d$) and standardized Morisita index ($I_p$) results by size class. Results are reported for species occurring in ten or more of the 240 sampled plots. $I_d$ reports values from 0 to $n$. The pattern is uniform if $0 < I_d < 1$, clumped if $1 < I_d < n$, and random if $I_d = 1$. $I_p$ reports values from -1.0 to +1.0. The pattern is random if $I_p = 0$, clumped if $I_p > 0$ and uniform if $I_p < 0$. “NA” is reported where there are one or less occurrences; “C” = clumped pattern; “U” = uniform pattern; “R” = random pattern. Pattern results marked with an asterisk (*) are likely unreliable and result of small sample size within that particular subset.

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<thead>
<tr>
<th>Species</th>
<th>$I_d$</th>
<th>$I_p$</th>
<th>Pattern</th>
<th>$I_d$</th>
<th>$I_p$</th>
<th>Pattern</th>
<th>$I_d$</th>
<th>$I_p$</th>
<th>Pattern</th>
<th>$I_d$</th>
<th>$I_p$</th>
<th>Pattern</th>
</tr>
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<tbody>
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<td>C</td>
<td>2.90</td>
<td>0.51</td>
<td>C</td>
<td>5.03</td>
<td>0.51</td>
<td>C</td>
<td>2.22</td>
<td>0.50</td>
<td>C</td>
</tr>
<tr>
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<td>C</td>
<td>6.83</td>
<td>0.54</td>
<td>C</td>
<td>4.78</td>
<td>0.51</td>
<td>C</td>
<td>7.90</td>
<td>0.52</td>
<td>C</td>
</tr>
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<td>Atriplex polycarpa</td>
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<td>C</td>
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<td>-0.05</td>
<td>U*</td>
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<td>26.78</td>
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<td>C</td>
</tr>
<tr>
<td>Cylindropuntia echinocarpa</td>
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<td>0.51</td>
<td>C</td>
<td>0.00</td>
<td>-0.05</td>
<td>U*</td>
<td>3.24</td>
<td>0.50</td>
<td>C</td>
<td>7.51</td>
<td>0.51</td>
<td>C</td>
</tr>
<tr>
<td>Encelia virginensis</td>
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<td>C</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>42.76</td>
<td>0.63</td>
<td>C</td>
<td>27.14</td>
<td>0.56</td>
<td>C</td>
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<tr>
<td>Ephedra nevadensis</td>
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<td>0.53</td>
<td>C</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
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<td>0.59</td>
<td>C</td>
<td>13.20</td>
<td>0.53</td>
<td>C</td>
</tr>
<tr>
<td>Ephedra torreyana</td>
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<td>0.51</td>
<td>C</td>
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<td>NA</td>
<td>NA</td>
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<td>C</td>
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<td>Gutierrezia species</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
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<td>C</td>
<td>38.41</td>
<td>0.59</td>
<td>C</td>
</tr>
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<td>C</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
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<td>0.35</td>
<td>C</td>
<td>3.23</td>
<td>0.50</td>
<td>C</td>
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<td>C</td>
<td>0.00</td>
<td>-0.07</td>
<td>U*</td>
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<td>C</td>
</tr>
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<td>NA</td>
<td>NA</td>
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<td>0.51</td>
<td>C</td>
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<td>0.51</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
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<td>0.54</td>
<td>C</td>
<td>22.45</td>
<td>0.55</td>
<td>C</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>3.24</td>
<td>0.29</td>
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<td>Psorothamnus fremontii</td>
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<td>0.52</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
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<td>NA</td>
<td>NA</td>
<td>10.70</td>
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<td>Xylorhiza tortifolia</td>
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<td>C</td>
<td>0.00</td>
<td>-0.05</td>
<td>U*</td>
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<td>0.54</td>
<td>C</td>
<td>23.78</td>
<td>0.55</td>
<td>C</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
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<td>-0.04</td>
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(Continued on next page)
Table 3.4. Morisita’s index ($I_d$) and standardized Morisita index ($I_p$) results by size class (continued).

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<thead>
<tr>
<th>Species</th>
<th>$I_d$</th>
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<th>Pattern</th>
<th>$I_d$</th>
<th>$I_p$</th>
<th>Pattern</th>
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<tr>
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<td>NA</td>
<td>NA</td>
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<td>-0.13</td>
<td>U*</td>
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<td>-0.04</td>
<td>U*</td>
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<td>NA</td>
<td>NA</td>
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<td>NA</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
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<td>Ephedra torreyana</td>
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<td>NA</td>
<td>NA</td>
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<td>NA</td>
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<td>NA</td>
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<td>NA</td>
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<td>-0.21</td>
<td>U</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Psorothamnus fremontii</td>
<td>8.27</td>
<td>0.51</td>
<td>C</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
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<tr>
<td>Xylorhiza tortifolia</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
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<td>Yucca schidigera</td>
<td>5.78</td>
<td>0.46</td>
<td>C</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
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</table>
Table 3.5. Morisita’s index ($I_d$) and standardized Morisita index ($I_p$) results by soil unit. Results are reported for species occurring in ten or more of the 240 sampled plots. $I_d$ reports values from 0 to $n$. The pattern is uniform if $0 < I_d < 1$, clumped if $1 < I_d < n$, and random if $I_d = 1$. $I_p$ reports values from -1.0 to +1.0. The pattern is random if $I_p = 0$, clumped if $I_p > 0$ and uniform if $I_p < 0$. “NA” is reported where there are one or less occurrences; “C” = clumped pattern; “U” = uniform pattern; “R” = random pattern. Pattern results marked with an asterisk (*) are likely unreliable and result of small sample size within that particular subset. The Weiser-Goodsprings Complex is not reported due to lack of data.

<table>
<thead>
<tr>
<th>Species</th>
<th>All plots</th>
<th>Arizo</th>
<th>Badland</th>
<th>Dalian-McCullough Complex</th>
</tr>
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<td>$I_d$</td>
<td>$I_p$</td>
<td>Pattern</td>
<td>$I_d$</td>
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<td><em>Ambrosia dumosa</em></td>
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<td>C</td>
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<td><em>Atriplex confertifolia</em></td>
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<td>C</td>
<td>NA</td>
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<td><em>Atriplex polycarpa</em></td>
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<td>C</td>
<td>0.00</td>
</tr>
<tr>
<td><em>Encelia virginensis</em></td>
<td>37.12</td>
<td>0.57</td>
<td>C</td>
<td>4.51</td>
</tr>
<tr>
<td><em>Ephedra nevadensis</em></td>
<td>16.75</td>
<td>0.53</td>
<td>C</td>
<td>0.00</td>
</tr>
<tr>
<td><em>Ephedra torreyana</em></td>
<td>6.85</td>
<td>0.51</td>
<td>C</td>
<td>NA</td>
</tr>
<tr>
<td><em>Gutierrezia species</em></td>
<td>33.76</td>
<td>0.57</td>
<td>C</td>
<td>8.06</td>
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<td><em>Hymenoclea salsola</em></td>
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<td>0.60</td>
<td>C</td>
<td>7.61</td>
</tr>
<tr>
<td><em>Krameria erecta</em></td>
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<td>0.50</td>
<td>C</td>
<td>8.70</td>
</tr>
<tr>
<td><em>Larrea tridentata</em></td>
<td>1.72</td>
<td>0.50</td>
<td>C</td>
<td>1.35</td>
</tr>
<tr>
<td><em>Lycium species</em></td>
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<td>0.51</td>
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<td>3.33</td>
</tr>
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<td>23.31</td>
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<td>C</td>
<td>NA</td>
</tr>
<tr>
<td><em>Opuntia basilaris</em></td>
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<td>0.24</td>
<td>C</td>
<td>NA</td>
</tr>
<tr>
<td><em>Psorothamnus fremontii</em></td>
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<td>0.52</td>
<td>C</td>
<td>NA</td>
</tr>
<tr>
<td><em>Xylorhiza tortifolia</em></td>
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<td>0.55</td>
<td>C</td>
<td>NA</td>
</tr>
<tr>
<td><em>Yucca schidigera</em></td>
<td>2.64</td>
<td>0.24</td>
<td>C</td>
<td>NA</td>
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</table>

(Continued on next page)
Table 3.5. Morisita’s index ($I_d$) and standardized Morisita index ($I_p$) results by soil unit (continued).

<table>
<thead>
<tr>
<th>Species</th>
<th>Las Vegas-DeStazo Complex</th>
<th>Las Vegas</th>
<th>Weiser-Wechech Association</th>
<th>Weiser</th>
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<td>$I_d$</td>
<td>$I_p$</td>
<td>Pattern</td>
<td>$I_d$</td>
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<td>0.53</td>
<td>C</td>
<td>4.23</td>
</tr>
<tr>
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<td>0.55</td>
<td>C</td>
<td>1.75</td>
</tr>
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<td>Atriplex polycarpa</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Cylindropuntia echinocarpa</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Encelia virginsensis</td>
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<td>NA</td>
<td>NA</td>
</tr>
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<td>C</td>
<td>NA</td>
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<td>0.52</td>
<td>C</td>
<td>1.62</td>
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<td>Gutierrezia species</td>
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<td>Hymenoclea salsola</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
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<tr>
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<td>1.89</td>
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<td>10.00</td>
</tr>
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<td>0.50</td>
<td>C</td>
<td>2.70</td>
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<tr>
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<td>0.52</td>
<td>C</td>
<td>2.08</td>
</tr>
<tr>
<td>Menodora spinescens</td>
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<td>0.54</td>
<td>C</td>
<td>8.82</td>
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<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Psorothamnus fremontii</td>
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<td>-0.10</td>
<td>U*</td>
<td>NA</td>
</tr>
<tr>
<td>Xylorhiza tortifolia</td>
<td>15.56</td>
<td>0.87</td>
<td>C</td>
<td>7.00</td>
</tr>
<tr>
<td>Yucca schidigera</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
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</table>
Table 3.6. Morisita’s index ($I_d$) and standardized Morisita index ($I_p$) results by vegetation association. Results are reported for species occurring in ten or more of the 240 sampled plots. $I_d$ reports values from 0 to $n$. The pattern is uniform if $0 < I_d < 1$, clumped if $1 < I_d < n$, and random if $I_d = 1$. $I_p$ reports values from -1.0 to +1.0. The pattern is random if $I_p = 0$, clumped if $I_p > 0$ and uniform if $I_p < 0$. “NA” is reported where there are one or less occurrences; “C” = clumped pattern; “U” = uniform pattern; “R” = random pattern. Pattern results marked with an asterisk (*) are likely unreliable and result of small sample size within that particular subset.

<table>
<thead>
<tr>
<th>Species</th>
<th>All plots</th>
<th>Ambrosia dumosa - Atriplex confertifolia Association</th>
<th>Ambrosia dumosa - Larrea tridentata: Upper Alluvial Fan Association</th>
<th>Ambrosia dumosa - Menodora spinescens Association</th>
</tr>
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Table 3.6. Morisita’s index ($I_d$) and standardized Morisita index ($I_p$) results by vegetation association (continued).

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<th>Larrea tridentata - Ambrosia dumosa Association</th>
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Table 3.7. Morisita’s index ($I_d$) and standardized Morisita index ($I_p$) results by geologic unit. Results are reported for species occurring in ten or more of the 240 sampled plots. $I_d$ reports values from $0$ to $n$. The pattern is uniform if $0 < I_d < 1$, clumped if $1 < I_d < n$, and random if $I_d = 1$. $I_p$ reports values from -1.0 to +1.0. The pattern is random if $I_p = 0$, clumped if $I_p > 0$ and uniform if $I_p < 0$. “NA” is reported where there are one or less occurrences; “C” = clumped pattern; “U” = uniform pattern; “R” = random pattern. Pattern results marked with an asterisk (*) are likely unreliable and result of small sample size within that particular subset.

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Table 3.7. Morisita’s index ($I_d$) and standardized Morisita index ($I_p$) results by geologic unit (continued).

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Table 3.8. L-funtion results for Transect 1. Results are presented for all species together, *Ambrosia dumosa* alone, and *Larrea tridentata* alone. Species dispersion pattern is presented as clumped, random, or uniform. Patterns were identified by observing the L-function plots (Appendix I).

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Table 3.9. L-function results for Transect 2. Results are presented for all species together, *Ambrosia dumosa* alone, and *Larrea tridentata* alone. Species dispersion pattern is presented as clumped, random, or uniform. Patterns were identified by observing the L-function plots (Appendix I).

<table>
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<tr>
<th>Plot</th>
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<th><em>Larrea tridentata</em></th>
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<td>Random, clumped when 0.8 &lt; t &gt; 1.0</td>
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</tr>
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<td>Random, clumped when 0.5 &lt; t &gt; 1.0 and 3.9 &lt; t &gt; 4.9</td>
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<td>Random, clumped when 0.9 &lt; t &gt; 1.2</td>
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<td>7</td>
<td>Random</td>
<td>Random</td>
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</tr>
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<td>8</td>
<td>Random, clumped when 1.25 &lt; t &gt; 1.5 and 2.4 &lt; t &gt; 2.6</td>
<td>Random, clumped when 0.5 &lt; t &gt; 3.3</td>
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<td>9</td>
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Table 3.10. Morisita’s index \((I_d)\) and standardized Morisita index \((I_p)\) overall and size class results for the transect data. Results \(I_d\) reports values from 0 to \(n\). The pattern is uniform if \(0 < I_d < 1\), clumped if \(1 < I_d < n\), and random if \(I_d = 1\). \(I_p\) reports values from -1.0 to +1.0. The pattern is random if \(I_p = 0\), clumped if \(I_p > 0\) and uniform if \(I_p < 0\). “NA” is reported where there are one or less occurrences; “C” = clumped pattern; “U” = uniform pattern; “R” = random pattern. Pattern results marked with an asterisk (*) are likely unreliable and result of small sample size within that particular subset.

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<th>(I_d)</th>
<th>(I_p)</th>
<th>Pattern</th>
<th>(I_d)</th>
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CHAPTER 4

BIOMASS AND ABUNDANCE PATTERNS AMONG PLANT COMMUNITIES IN THE MOJAVE DESERT: EXAMINING THE ROLE OF SELF-THINNING

Abstract. The self-thinning rule, a theory based on plant-plant competitive interactions, predicts a negative relationship between mean plant biomass and plant density. Ecologists have begun to question the applicability of the classic self-thinning rule and competition in arid environments, citing that facilitative interactions may cause the relationship to be weaker or perhaps positive. We investigated the relationship between plant size and abundance within and among plant communities growing on a Mojave Desert bajada. The objectives of this study were twofold. The first was to examine the patterns of biomass and abundance within and among plant communities growing on different soil types and geologic substrates. Overall, we saw biomass and abundance patterns change significantly between soil, geology, and plant community associations. The second objective was to ascertain if the entire bajada community, and Larrea tridentata and Ambrosia dumosa individually, exhibited the self-thinning relationship. Our results did not provide evidence of self-thinning relationships, but instead showed significant positive relationships in the log-log plots of plot density vs. total plot volume for all species together, for L. tridentata alone, and A. dumosa alone. Our results support the strong role of substrate in determining plant community structure as well as theories predicting that facilitation is a dominant component in arid plant communities.
INTRODUCTION

The relationship between body size and abundance has been a central focus in ecology. For terrestrial plants, total abundance per unit area has been shown to decline with increasing mean plant size (Enquist et al. 1998, Belgrano et al. 2002, White et al. 2007). This well-known relationship is commonly referred to as the self-thinning rule and is depicted by a log-log plot of mean plant biomass vs. plant density (Antinovics and Levin 1980, Westoby 1984, Weller 1987, Kerkhoff and Enquist 2007, White et al. 2007). Specifically, plant density decreases linearly as plant mass increases, with a predicted slope between $-3/2$ and $-4/3$ (Westoby 1984, Weller 1987, Damuth 1998, Enquist et al. 1998, Enquist and Niklas 2001, Belgrano et al. 2002, Kerkhoff and Enquist 2006, 2007). This relationship has been demonstrated in both single and mixed species stands and across 23 orders of magnitude (Enquist et al. 1998). The self-thinning rule has been described as the only rule or law in plant ecology (Weller 1989).

The thinning rule is based on the assumption that plants compete for limited resources within a given area and resource supply limits community carrying capacity (Enquist et al. 1998, White et al. 2007, Ernest et al. 2009). Assuming that plants grow until they are limited by resources, and larger plants use more resources within a community, an increase in plant size should necessitate a decrease in density (Van Valen 1973, Kerkhoff and Enquist 2007). This is also known as density-dependent mortality (White 1981). For self-thinning to occur, it is assumed that the community is in a demographically steady state at carrying capacity and total resource use is in a steady

While the term “self-thinning” has been used to describe both intra and interspecific stands, it is important to note that the classic self-thinning rule was originally used to describe intraspecific stands (Lonsdale 1990). Classic self-thinning describes a dynamic relationship between biomass and density of a single species stand over time (Weller 1989, Scrosati 2005). While the self-thinning rule is often used to describe the interspecific relationship between biomass and density, it is a static relationship showing a single moment of time (Weller 1989, Scrosati 2005).

There has been considerable discussion regarding the relationship between the slope of the self-thinning relationship and which size variables are to be analyzed. Both the mean plant biomass and total stand biomass have been reported in the literature (Scrosati 2005). When plotting mean plant biomass against density, the slope is predicted to be -3/2 to -4/3, depending on how it was derived (Westoby 1981, Weller 1987, 1989, Enquist et al. 1998). However, if total stand biomass per unit area is plotted against density per unit area, the slope is predicted to be -1/3 to -1/2 (Westoby 1981, Weller 1989, Enquist et al. 1998). Weller (1987) states that total stand biomass should be preferred over mean plant biomass in the calculation of thinning lines. He explains that average plant size can be statistically misleading because average size increases when small individuals die, even if the survivors do not actually grow whereas, total stand biomass increases only through growth and decreases with mortality.
While there has been some debate regarding the numerical value of the self-thinning slope (Enquist et al. 1998, Dai et al. 2009, Ernest et al. 2009, Wang et al. 2013), recent research has questioned the applicability of the thinning rule in arid environments (Deng et al. 2006, Lin et al. 2013, Wang et al. 2013). The self-thinning relationship is a consequence of competitive interactions within a population or community that is at carrying capacity with a steady state of resource use and supply. Given that water is thought to be the principal limiting factor in desert ecosystems, classic theory predicts that plants must compete with neighbors for its uptake. However, it has been suggested that facilitative, rather than competitive, interactions may be more prevalent in harsh environments whereby neighbors ameliorate abiotic stress (Bertness and Callaway 1994, Stachowicz 2001, Bruno et al. 2003, Armas & Pugnaire 2005, Brooker et al. 2008, Malkinson and Tielbörger 2010). Furthermore, resource supply is not steady in arid environments (Fowler 1986, Chesson et al. 2004, Schwinning and Sala 2004). Fluctuating resource levels may cause variations in the size and carrying capacity of a population which in turn might stimulate either competitive or facilitative interactions between plants. To add to the complexity, water availability is soil specific. Subtle differences in soil texture, age, and horizon development may lead to large differences in the amount of water that can be stored and absorbed (Yang and Lowe 1956, MacMahon and Wagner 1985, Hamerlynck et al. 2000, Hamerlynck et al. 2002, Hamerlynck et al. 2004, McAuliffe et al. 2007, Ignace and Huxman 2009, Webb 2009, Schwinning et al. 2011). Soil hydrologic properties thus influence the patterns of biomass and abundance in arid plant communities.
Those investigating the self-thinning rule in arid environments have shown that the thinning relationship is weaker under increased aridity (Deng et al. 2006, Chu et al. 2008, Lin et al. 2013) and have proposed that facilitative interactions may offset or delay the negative effects of competition (Deng et al. 2006, Chu et al. 2008, 2009, 2010). Deng et al. (2006) postulated a positive relationship where facilitation is commonly observed, due to the positive effect of neighboring plants. To our knowledge, few studies have observed the proposed self-thinning relationship in arid environments. Allen et al. (2008) reported a negative relationship between \textit{Larrea tridentata} density and average plant size with a slope of -3/4, thereby supporting the self-thinning rule. They assert that their study is the first to document such a relationship for a single species in a water limited ecosystem and use this as evidence that xeric plant populations are regulated by competition.

This study will explore the relationship between biomass and abundance within and among plant communities growing on a Mojave Desert bajada. Our first objective is to determine if biomass and abundance patterns are significantly different between plant communities. Because soil and geology serve as the resource template for arid plant communities, we will compare biomass and density patterns between communities growing on different soil types and geologic substrates. We will give special focus to the dominant shrubs, \textit{Larrea tridentata} and \textit{Ambrosia dumosa}, which cover approximately 70\% of the Mojave Desert (MacMahon 2000, Rundel and Gibson 1996). We expect that changes in biomass and abundance patterns will coincide with changes in soil and geologic types with more arid substrates supporting fewer and smaller individuals.
Our second objective is to ascertain if the entire bajada community, and \textit{L. tridentata} and \textit{A. dumosa} individually, exhibit the self-thinning relationship. If the self-thinning law if evident and competitive interactions are structuring this site, we expect to see larger biomass values coinciding with lower densities and smaller biomass values corresponding to greater densities. Understanding how biomass is partitioned within communities may offer insights into the mechanisms structuring communities (Enquist and Niklas 2001, White et al. 2007).

METHODS

\textit{Study area}

The Upper Las Vegas Wash Conservation Transfer Area (ULVWCTA), Nevada, consists of a 7,400 ha land parcel of Mojave Desert vegetation on alluvial fan (bajada) and basin floor deposits derived from the Spring and Sheep Mountains. The area sits north of Las Vegas and is transected by a complex of Pleistocene spring deposits and their attendant washes. A research team from Utah State University was tasked with creating vegetation and soils maps of the ULVWCTA. This effort identified seven vegetation associations and eight soil map units across the site (MacMahon et al. 2008). These maps, in addition to geologic data obtained from a USGS map (1:100,000 Geologic and Geophysical maps of the Las Vegas 30’ X 60’ Quadrangle, Clark and Nye Counties, Nevada, and Inyo County, California (Page et al. 2005), were used in the spatial analyses. Tables 4.1, 4.2, and 4.3 provide lists and descriptions of each vegetation association, soil type, and geologic unit respectively.
Vegetation sampling

The vegetation data collected for the MacMahon et al. (2008) mapping effort was used as the first dataset for spatial analysis. A stratified sampling design provided a total of 240 plots sampled across the ULVWCTA. Two strata, based on broad geomorphic categories, were identified. The first was defined as alluvial fan/wash and totaled 5,270 ha (71%) of the ULVWCTA. The second stratum (2,130 ha, 29%) was defined as basin floor/spring deposit, and was associated with past ground-water discharge (evidenced by highly calcareous spring deposits) and lacustrine sediments.

A total of 240 plots were sampled across the ULVWCTA. Initially, the mapping data consisted of 163 sample plots that were systematically distributed along 13 north-south transects spaced 2000 meters apart. Vegetation data were collected every 100 meters in the basin floor/spring deposit stratum and every 500 meters in the alluvial fan/wash stratum. Preliminary evaluation of these data indicated inadequate coverage of the area, so an additional 77 sample plots were established and surveyed to increase sampling intensity where vegetation variation was greater, and where spectral reflectance data from Landsat 7 and ASTER satellites suggested greater complexity in geomorphic surfaces and vegetation.

Each sample plot consisted of the area of a circle with a 10-m radius. Each circular plot was divided into quarters by an east-west and a north-south line. One quarter of each plot was used to survey vegetation. The quarter chosen for sampling was rotated in a clockwise manner from one sample plot to the next. Vegetation data were collected for woody perennials only. For each plant within the sample quarter, the
height, width in two directions (the longest width and the width perpendicular to this), and species were recorded.

Analytical methods

Biomass and abundance patterns between plant communities growing on different soil types and geologic substrates were compared using one-way analysis of variance (ANOVA). Plant volume was used as a non-destructive proxy for biomass. Total plant volume and density, L. tridentata volume and density, and A. dumosa volume and density were compared in each vegetation association, soil type, and geologic substrate. With the exception of L. tridentata, shrub volume was calculated as an oblate ellipsoid (Phillips and MacMahon 1981). The volume for L. tridentata was calculated as an inverted elliptical cone (Chew and Chew 1965, Schlesinger and Jones 1984). Shrub density was calculated as the number of individuals/plot. The area sampled in each plot (1/4 of the circle) was 78.5m². All volume and density measures were cube root transformed to meet assumptions of normality. Relevant post-hoc pairwise comparisons were made using the Tukey-Kramer procedure. All values were reported as back-transformed means with standard errors and significance was determined at $P < 0.05$. Analyses were performed using SAS software, Version 9.2 of the SAS System for Windows (SAS Institute Inc. 2011).

The relationship between plant size (volume) and abundance (density) was assessed using Ordinary Least Squares Regression (OLS). The log of plot density (dependent variable) was linearly regressed on both the log of total plot volume and on the log of mean plot volume (independent variables). While many size-abundance studies use mass as the size metric, it is also customary to use volume as it is directly
proportional to mass (White et al. 2007). Analyses were performed in R (version 2.13.2; R Development Core Team, Vienna, Austria 2011). Plots devoid of plant material were omitted from the analyses.

RESULTS

A total of 6,759 individual plants (39 different species) were identified and measured within the 240 mapping plots. Thirteen plots did not contain vegetation. Appendix A provides a list of all species that were identified during field work on the ULVWCTA. Appendix B provides a list of all the mapping plots with corresponding elevation, vegetation associations, soil types, and geologic units. Appendix C provides a list and frequency count for all species identified in the mapping plots. The Weiser-Goodsprings soil complex was not included in the analyses as it only had one sampling plot.

One-way analysis of variance. There was a significant effect of soil map unit on plot volume (ANOVA, $F_{(6, 232)} = 26.38, P < .0001$) and plot density (ANOVA, $F_{(6, 232)} = 17.29, P < .0001$). Post-hoc comparisons using the Tukey-Kramer test indicated that Arizo ($M = 5.14, SE = 0.80$), Weiser ($M = 4.09, SE = 0.57$), and Weiser-Wechech ($M = 3.84, SE = 0.46$) had the greatest shrub volume while the Badland ($M = 0.29, SE = 0.13$), Las Vegas-DeStazo Complex ($M = 1.08, SE = 0.36$), and Las Vegas ($M = 0.30, SE = 0.16$) had the least. Shrub density was greatest on the Arizo ($M = 0.43, SE = 0.06$), Las Vegas-DeStazo Complex ($M = 0.44, SE = 0.08$), and the Weiser-Wechech ($M = 0.43, SE = 0.04$) types while the Badland ($M = 0.06, SE = 0.02$), Las Vegas ($M = 0.15, SE = 0.04$),
and Weiser ($M = 0.21$, $SE = 0.03$) were less dense. Figure 4.1 provides a graphical summary of these results.

The effects of soil type on volume and density were also significant when *L. tridentata* and *A. dumosa* were analyzed individually. *L. tridentata* volume (ANOVA $F_{(6, 197)} = 11.35$, $P < .0001$) and density (ANOVA, $F_{(6, 197)} = 10.71$, $P < .0001$) differed by soil type as did *A. dumosa* volume (ANOVA, $F_{(6, 176)} = 3.63$, $P = .002$) and density (ANOVA, $F_{(6, 176)} = 6.20$, $P < .0001$). Post hoc comparisons showed that *L. tridentata* volume was greatest on the Arizo ($M = 2.84$, $SE = 0.45$), Weiser ($M = 4.21$, $SE = 0.54$), and the Weiser-Wechech ($M = 2.60$, $SE = 0.32$) types and least on the Las Vegas-DeStazo Complex ($M = 0.47$, $SE = 0.20$). *L. tridentata* density was greatest on the Weiser ($M = 0.09$, $SE = 0.01$) and the Weiser-Wechech ($M = 0.09$, $SE = 0.01$) types and lowest on the Badland ($M = 0.03$, $SE = 0.01$), Las Vegas ($M = 0.03$, $SE = 0.01$), and Las Vegas-DeStazo Complex ($M = 0.03$, $SE = 0.01$) types. *A. dumosa* volume was greatest on the Weiser-Wechech ($M = 0.53$, $SE = 0.07$) soil and least on the Badland ($M = 0.15$, $SE = 0.07$) soil. *A. dumosa* density was greatest on the Las Vegas-DeStazo Complex ($M = 0.31$, $SE = 0.07$) and less dense on the Badland ($M = 0.09$, $SE = 0.04$) and Weiser ($M = 0.07$, $SE = 0.02$) soils. Figure 4.1 provides a graphical summary of these results.

Considering all species, there was a significant effect of geologic type on plot volume (ANOVA, $F_{(6, 233)} = 21.91$, $P < .0001$) and plot density (ANOVA, $F_{(6, 233)} = 6.45$, $P < .0001$). Post-hoc comparisons using the Tukey-Kramer test indicated that shrub volume was greatest on the Qayy unit ($M = 4.72$, $SE = 0.68$) and lowest on the Qscd unit ($M = 0.52$, $SE = 0.12$) while density was greatest on the Qayy unit ($M = 0.39$, $SE = 0.05$)
and lowest on the Qsu unit ($M = 0.05, SE = 0.07$). Figure 4.2 provides a graphical summary of these results. *L. tridentata* volume (ANOVA, $F_{(5, 197)} = 7.70, P < .0001$) and density (ANOVA, $F_{(5, 197)} = 10.95, P < .0001$) varied between geologic types, however post hoc tests did not distinguish between groups. *A. dumosa* volume (ANOVA, $F_{(5, 177)} = 1.28, P = 0.273$) and density (ANOVA, $F_{(5, 177)} = 0.62, P = 0.687$) were not affected by geologic type. Figure 4.2 provides a graphical summary of these results.

There was a significant effect of vegetation association on plot volume (ANOVA, $F_{(6, 232)} = 27.56, P < .0001$) and plot density (ANOVA, $F_{(6, 232)} = 15.50, P < .0001$). Post-hoc comparisons using the Tukey-Kramer test indicated that shrub volume was greatest on the *Atriplex polycarpa* - *Ambrosia dumosa* ($M = 5.81, SE = 1.08$) and *Larrea tridentata* - *Ambrosia dumosa* ($M = 3.40, SE = 0.27$) Associations and least on *Ambrosia dumosa* - *Atriplex confertifolia* ($M = 0.35, SE = 0.12$) and Badlands ($M = 0.004, SE = 0.04$) Associations. Plant density was greatest on the *Ambrosia dumosa* - *Menodora spinescens* Association ($M = 0.93, SE = 0.20$) and least on the Badlands ($M = 0.02, SE = 0.02$) and *Larrea tridentata* Association ($M = 0.03, SE = 0.02$). Figure 4.3 provides a graphical summary of these results.

The effect of vegetation association on volume and density was also significant when *L. tridentata* and *A. dumosa* were analyzed individually. *L. tridentata* volume (ANOVA $F_{(5, 197)} = 9.86, p < .0001$) and density (ANOVA, $F_{(5, 197)} = 13.88, P < .0001$) differed by vegetation association as did *A. dumosa* volume (ANOVA, $F_{(5, 177)} = 3.58, P < .004$) and density (ANOVA, $F_{(5, 177)} = 4.21, P = .001$). Post hoc comparisons showed that *L. tridentata* volume was greatest on the *Atriplex polycarpa* - *Ambrosia dumosa* ($M =
2.63, \( SE = 0.65 \) and *Larrea tridentata* - *Ambrosia dumosa* \((M = 2.82, SE = 0.23)\) Associations and least on the *Ambrosia dumosa* - *Atriplex confertifolia* Association \((M = 0.56, SE = 0.22)\). *L. tridentata* density was greatest on the *Larrea tridentata* - *Ambrosia dumosa* Association \((M = 0.08, SE = 0.005)\) and least on the *Ambrosia dumosa* - *Atriplex confertifolia* \((M = 0.02, SE = 0.005)\) and *Larrea tridentata* \((M = 0.02, SE = 0.008)\) associations. Post hoc tests for *A. dumosa* volume did not show differences between vegetation associations. *A. dumosa* density was greatest on the *Ambrosia dumosa* - *Menodora spinescens* Association \((M = 0.53, SE = 0.15)\) and least on the *Larrea tridentata* Association \((M = 0.05, SE = 0.08)\). Figure 4.3 provides a graphical summary of these results.

*Ordinary least squares regression.* The log-log plot of plot density vs. total plot volume revealed a significant positive relationship when all species were analyzed together \((F_{(1,222)} = 64.13, P < .0001, R^2 = 0.221)\), for *L. tridentata* alone \((F_{(1,201)} = 156.7, P < .0001, R^2 = 0.435)\), and *A. dumosa* alone \((F_{(1,182)} = 419.1, P < .0001, R^2 = 0.696)\) (Figure 4.4). The log-log of plot density vs. mean plot volume was not significant for all species analyzed together \((F_{(1,222)} = 3.509, P = 0.062, R^2 = 0.011)\) and for *L. tridentata* alone \((F_{(1,201)} = 0.00002, P = 0.996, R^2 = -0.005)\) (Figure 4.5). The plot for *A. dumosa* alone had a significant P-value, however the \(R^2\) value indicates that the relationship is extremely weak to nonexistent \((F_{(1,182)} = 7.48, P = 0.007, R^2 = 0.034)\) (Figure 4.5).
DISCUSSION

The objective of this study was to examine the relationship between biomass and abundance patterns of woody perennial species growing on the ULVWCTA and compare patterns between soil types, geologic types, and plant communities. Results from ANOVA analyses and post-hoc comparisons using the Tukey-Kramer test show shrub volume and density measurements to be broadly split between the two prominent geomorphic categories (parent material) present on the ULVWCTA: alluvium and spring deposits. This agrees with previous investigations that have also exposed this distinction (see Chapters 2 and 3). In general, the alluvium sites are younger, composed of larger particles with weakly developed horizons located on bajada fans or active channels. Alluvial sites typically have more moisture available than lower elevation spring deposits sites (playas). Prominent alluvium soil types include Weiser, the Dalian-McCullogh Complex, the Weiser-Wechech Association, and Arizo. Geologic types associated with these locations include Qay, Qayo, and Qayy. Vegetation associations include the *Larrea tridentata* - *Ambrosia dumosa* Association, *Atriplex polycarpa* - *Ambrosia dumosa* Association, and the *Ambrosia dumosa* - *Larrea tridentata*: Upper Alluvial Fan Association.

Spring deposit sites are older and composed of smaller soil particles with more horizon development, some of which are cemented with calcite. These areas are associated with past ground water discharge and include the Las Vegas and Las Vegas-Destazo Complex soil types. The prominent geologic unit is Qscd and vegetation associations include *Ambrosia dumosa* - *Atriplex confertifolia* Association, *Ambrosia*
dumosa - *Menodora spinescens* Association, Badlands, and the *Larrea tridentata* Association. Spring deposit sites and their associated soil, geology, and vegetation types are generally hotter, drier, and lower in elevation than alluvium sites.

*One-way analysis of variance.* Shrub volume measurements were greatest on alluvial soils, geology, and vegetation associations. These results are consistent with our prediction that changes in biomass patterns would coincide with changes in soil and geologic types with more arid, spring deposit substrates supporting smaller individuals. When all woody perennial species were analyzed together, shrub volume was greatest on alluvium soils (Arizo, Weiser, and Weiser-Wechech), geology (Qayy), and vegetation (*Atriplex polycarpa - Ambrosia dumosa* and *Larrea tridentata - Ambrosia dumosa* Associations). Shrub volume was least on spring deposit soils (Badland, Las Vegas-DeStazo Complex, and Las Vegas), geology (Qscd), and vegetation (*Ambrosia dumosa - Atriplex confertifolia* and Badlands Associations). *L. tridentata* volume was greatest on alluvial soil types (Arizo, Weiser, and Weiser-Wechech) and vegetation associations (*Atriplex polycarpa - Ambrosia dumosa* and *Larrea tridentata - Ambrosia dumosa* Associations) and least on a spring deposit soil (Las Vegas-DeStazo Complex) and vegetation associations (*Ambrosia dumosa - Atriplex confertifolia* Association). Post-hoc comparisons for *L. tridentata* volume did not reveal significant differences between geologic types. *A. dumosa* volume was greatest on alluvium soil (Weiser-Wechech) and least on spring deposit soil (Badland). Post-hoc comparisons for *A. dumosa* volume did not reveal significant differences between geologic types or vegetation associations.
Changes in shrub density measurements were not as straightforward as predicted with shrub density varying between spring deposit and alluvium soil and vegetation types. When all species were analyzed together, the greatest shrub densities were found on both alluvium (Arizo and Weiser-Wechech) and spring deposit (Las Vegas-DeStazo Complex) soil types, alluvium geology (Qayy), and a spring deposit vegetation association (*Ambrosia dumosa - Menodora spinescens* Association). The lowest shrub densities were found on both alluvium (Weiser) and spring deposit (Badland and Las Vegas) soil types and only on spring deposit geology (Qscd) and vegetation associations (Badlands and *Larrea tridentata* Associations). *L. tridentata* density was greatest on alluvial soil types (Weiser and Weiser-Wechech) and vegetation associations (*Larrea tridentata - Ambrosia dumosa* Association) and least on the spring deposit soils (Badland, Las Vegas, and Las Vegas-DeStazo Complex) and vegetation associations (*Ambrosia dumosa - Atriplex confertifolia* and *Larrea tridentata* Associations). Post-hoc comparisons for *L. tridentata* density did not reveal significant differences among geologic groups. *A. dumosa* density was greatest on the spring deposit soil (Las Vegas-DeStazo Complex) and vegetation association (*Ambrosia dumosa - Menodora spinescens* Association) and least on spring deposit soil (Badland) and vegetation association (*Larrea tridentata* Association). Post-hoc comparisons for *A. dumosa* density did not reveal significant differences between geologic types. The high densities occurring on the spring deposit soil (Las Vegas-DeStazo Complex) and vegetation association (*Ambrosia dumosa - Menodora spinescens* Association) are result of the high numbers of *A. dumosa* individuals growing in these areas.
Overall, our results are consistent with literature citing soil development as one of the strongest predictors of plant community structure in arid environments (see Chapter 2). Generally, shrubs grew larger on alluvial sites with more potential moisture availability. There was a distinction between the two dominant species with *L. tridentata* having greater volume and density on alluvial substrates and *A. dumosa* having greater volume on alluvium but greater density on spring deposits. Similar to our observations, *L. tridentata* has been reported to dominate on younger, weakly developed, Holocene aged soils with gravelly alluvium as opposed to older, more developed, Pleistocene aged soils with possible calcic and argillic horizons (McAuliffe 1994, Miller and Huenneke 2000, Hamerlynck et al. 2002, McAuliffe et al. 2007, Hamerlynck and McAuliffe 2010). Schenk et al. (2003) noted the distinction between habitats for *L. tridentata* and *A. dumosa* finding the density, cover, and biomass of *L. tridentata* to be greater on alluvium soils while the density, cover, and biomass of *A. dumosa* was greater on finer grained soils. Hamerlynck et al. (2002) also found the density of *A. dumosa* to increase with soil horizon development. *A. dumosa* is a more shallow rooted, shorter lived, drought deciduous, and natural colonizer compared to *L. tridentata*, which could explain the higher densities observed on the shallow spring deposit soils.

*Ordinary Least Squares Regression.* While the results of our ANOVA analyses agreed with our predictions and evidence of previous investigations, the results from our regression analysis do not agree with classic self-thinning models. On the contrary, the log-log plot of plot density vs. total plot volume revealed a significant positive relationship when all species were analyzed together, for *L. tridentata* alone, and *A.
*dumosa* alone. Based on the recommendations provided by Weller (1987) we will focus our discussion on the relationship between total plot biomass vs. density rather than mean plot biomass vs. density.

The self-thinning rule is based on the assumption that plants are competing for limited resources within a given area and resource supply limits community carrying capacity (Enquist et al. 1998, White et al. 2007, Ernest et al. 2009). It is presumed that the community is in a demographically steady state at carrying capacity and total resource use is in a steady state with resource supply for self-thinning to occur. Based on these assumptions, we could simply conclude that the plant communities on the ULVWCTA violate these assumptions and self-thinning isn’t occurring. However, our regression models may provide evidence to a long standing debate in desert plant ecology.

clumped distributions into random ones, and random distributions into uniform ones, with uniform distribution originating from competition for water during long droughts. Based on this hypothesis, smaller plants should show more clumping patterns while larger individuals should tend toward uniformity (Philips and MacMahon 1981, Cody 1986, Skarpe 1991, Haase et al. 1996).

Despite the long held notion that plants must compete for limited water resources, there has been little evidence to support this hypothesis. Historically, clumped and random patterns have been detected more often in the desert southwest (Barbour 1969, Woodell et al. 1969, Barbour and Diaz 1973, Philips and MacMahon 1981, Schlesinger and Jones 1984, Cody 1986, Fowler 1986, Manning and Barbour 1988, Smith 1997, Eccles et al. 1999, Rayburn et al. 2011, see Chapter 3). There have only been a few reported cases of uniformity seen in *L. tridentata* (Barbour 1969, Woodell et al. 1969, Fonteyn and Mahall 1981, Philips and MacMahon 1981, Schlesinger and Jones 1984, see Chapter 3), many of which have been challenged on the premise of methodological and statistical inadequacies (Anderson 1971, Barbour 1973, King and Woodell 1973, Ebert and McMaster 1981, King and Woodell 1984, Prentice and Werger 1985, Fowler 1986, King and Woodell 1987, Cox 1987). In addition to methodological difficulties, care must be taken in inferring causation given the many different processes that may generate the same spatial patterns (Perry et al. 2002, Schenk et al. 2003, Escudero et al. 2005, Miriti 2006).

Given the frequency of evidence for facilitation on the ULVWCTA and for arid environments in general, it is possible that the positive relationship observed in the log-
log plot of total plot volume vs. plot density provides added evidence to the facilitation vs. competition debate. Theoretically, this plot shows that as more shrubs are packed into a plot, volume increases rather than decreases as it would under competitive forces. These results imply an overall positive effect from increased density, thus backing the proposal of Deng et al. (2006) who proposed a positive relationship between biomass and density where facilitation is commonly observed and others who proposed that facilitative interactions may offset the negative effects of competition thereby rendering the thinning relationship weaker under increased aridity (Deng et al. 2006, Chu et al. 2008, 2009, Lin et al. 2013). This may also provide evidence for the stress gradient hypothesis under which facilitative, rather than competitive, interactions are more prevalent in harsh environments.

The log-log plots of plot density vs. total plot volume for *L. tridentata* alone, and *A. dumosa* alone corroborate earlier work with these species. The strong positive relationship detected between plot density and total plot volume for *A. dumosa* supports a long line of evidence showing a prevalence of clumped patterns (i.e. facilitation) in *A. dumosa* (Fonteyn and Mahall 1981, Schlesinger and Jones 1984, Miriti 2006, see Chapter 3). While the relationship between plot density and total plot volume for *L. tridentata* is somewhat weaker than that for *A. dumosa*, this supports observations of mostly clumped and random dispersion patterns seen in *L. tridentata* with few instances of uniformity (i.e. possible self-thinning). Miller and Huenneke (2000) also observed a positive relationship between total biomass and density for *L. tridentata*. Our results do not agree with those of Allen et al. (2008) or Chew and Chew (1965) who reported a negative relationship.
between *L. tridentata* density and plant size (in the Chihuahuan and Sonoran Deserts, respectively.

While we saw overall significant positive relationships on the log-log plots of plot density vs. total volume, the results from the log-log plot of plot density vs. mean plot volume were generally insignificant. The results from these analyses showed that there were essentially no relationships between plot density vs. mean plot volume for all species analyzed together, for *L. tridentata* alone, and for *A. dumosa* alone. Although insignificant, these results are also contradictory with the classic self-thinning model and provide meaningful information regarding the relationship between biomass and abundance in arid environments. While they don’t provide evidence of facilitation like the plots of plot density vs. total plot volume, they may provide additional confirmation that competition isn’t acting as the prevailing plant-plant interaction.

The objectives of this study were twofold. The first was to examine the patterns of biomass and abundance within and among plant communities growing on different soil types and geologic substrates. Overall, we saw biomass and abundance patterns change significantly between soil, geology, and plant community associations, with soil and parent material driving these patterns. These findings support previous work citing soil development as one of the strongest predictors of plant community structure in arid environments.

The second objective was to determine if the bajada community, and *L. tridentata* and *A. dumosa* individually, exhibited the self-thinning relationship. Our results did not provide evidence of self-thinning relationships, but instead showed significant positive
relationships in the log-log plots of plot density vs. total plot volume for all species together, for *L. tridentata* alone, and *A. dumosa* alone. In light of the numerous studies providing evidence of possible facilitative interactions, we feel comfortable adding our findings to the collection of results leading plant ecologists to consider that facilitative rather than competitive interactions are the dominant biotic force shaping arid plant communities. Given that plants in arid environments are known to have an increased root:shoot ratio (Casper et al. 2003), future studies should investigate the relationship between root biomass and abundance. The belowground space between desert perennials has been said to be saturated with roots and may resemble a closed canopy like the plant communities measured in traditional self-thinning studies. It is possible that the log-log relationship between root biomass and density may provide different results.

In addition to adding clarification in the facilitation vs. competition debate, this research aids in understanding the roles of biotic vs. abiotic regulation in arid environments. Our results add to the mounting evidence which supports the large role that soil and geologic properties take in generating biomass and abundance patterns in arid plant communities. Combining this knowledge with the accumulating documentation of facilitative interactions, we propose that abiotic pressure, primarily soil available moisture, is the prevailing driver of arid plant community structure. Under this scenario, facilitation is seen as the dominant biotic force to offset abiotic pressure. Understanding the relationship between abiotic factors and plant-plant interactions is essential in making careful conservation and management decisions for desert ecosystems.
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LITERATURE CITED


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<tr>
<th>Vegetation Association</th>
<th>Description</th>
<th>Area (ha)</th>
<th>Elevation (m)</th>
<th>Number of plots sampled</th>
<th>Richness</th>
<th>Density (n/ha)</th>
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<td><em>Larrea tridentata</em> - <em>Ambrosia dumosa</em> Association</td>
<td><em>Larrea tridentata</em> and <em>Ambrosia dumosa</em> compose ≥70% of the relative density</td>
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<td>659 to 929</td>
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<td><em>Larrea tridentata</em> Association</td>
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<td>729 to 828</td>
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<td><em>Atriplex polycarpa</em> - <em>Ambrosia dumosa</em> Association</td>
<td><em>Atriplex polycarpa</em> and <em>Ambrosia dumosa</em> dominate in wet, active, and dry washes</td>
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<td><em>Ambrosia dumosa</em> and <em>Menodora spinescens</em> make up the greatest shrub density in the basin floor</td>
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<td>2612</td>
</tr>
</tbody>
</table>

Table 4.1. Vegetation associations of the ULVWCTA.
Table 4.2: Soil map units of the ULVWCTA.

<table>
<thead>
<tr>
<th>Soil</th>
<th>Parent material</th>
<th>Landform</th>
<th>Drainage class</th>
<th>(Ksat)*</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizo</td>
<td>Mixed alluvium</td>
<td>Channels</td>
<td>Excessively drained</td>
<td>High to very high (5.95 to 19.98 in/hr)</td>
<td>Very gravelly loamy sand</td>
</tr>
<tr>
<td>Dalian-McCullough Complex</td>
<td>Alluvium derived from limestone and dolostone</td>
<td>Fan skirts</td>
<td>Well drained</td>
<td>High (1.98 to 5.95 in/hr)</td>
<td>Very gravelly fine sandy loam</td>
</tr>
<tr>
<td>Las Vegas</td>
<td>Alluvium derived from limestone</td>
<td>Basin-floor remnants</td>
<td>Well drained</td>
<td>Very low (0 in/hr)</td>
<td>Gravelly fine sandy loam</td>
</tr>
<tr>
<td>Las Vegas-DeStazo Complex</td>
<td>Alluvium derived from limestone</td>
<td>Alluvial flats</td>
<td>Well drained</td>
<td>Very low (0 in/hr)</td>
<td>Gravelly fine sandy loam</td>
</tr>
<tr>
<td>Weiser-Wechech Association</td>
<td>Alluvium derived from limestone and dolomite</td>
<td>Fan remnants</td>
<td>Well drained</td>
<td>Moderately high to high (0.57 to 5.95 in/hr)</td>
<td>Extremely gravelly fine sandy loam</td>
</tr>
<tr>
<td>Weiser</td>
<td>Alluvium derived from limestone and dolomite</td>
<td>Fan remnants</td>
<td>Well drained</td>
<td>High (1.98 to 5.95 in/hr)</td>
<td>Extremely gravelly fine sandy loam</td>
</tr>
<tr>
<td>Weiser-Goodsprings Complex</td>
<td>Alluvium derived from limestone and dolomite</td>
<td>Fan remnants</td>
<td>Well drained</td>
<td>High (1.98 to 5.95 in/hr)</td>
<td>Extremely gravelly fine sandy loam</td>
</tr>
<tr>
<td>Badland</td>
<td>Mixed alluvium over lacustrine</td>
<td>Hills on alluvial flats</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Ksat=capacity of the most limiting layer to transmit water
<table>
<thead>
<tr>
<th>Unit*</th>
<th>Parent Material</th>
<th>Age</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Qai</td>
<td>Intermediate fan alluvium</td>
<td>Late and middle Pleistocene</td>
<td>Cemented alluvial-fan gravel, with interbedded sand; poorly to moderately well sorted</td>
</tr>
<tr>
<td>Qay</td>
<td>Young fan alluvium</td>
<td>Holocene and latest Pleistocene</td>
<td>Noncemented alluvial-fan gravel and sand with weakly developed soil.</td>
</tr>
<tr>
<td>Qayo</td>
<td>Older young alluvium</td>
<td>Holocene and latest Pleistocene</td>
<td>Noncemented gravel and sand with weakly developed soil of alluvial-fan remnants</td>
</tr>
<tr>
<td>Qayy</td>
<td>Youngest alluvium</td>
<td>Holocene</td>
<td>Noncemented alluvial-fan gravel and sand of intermittently active wash complexes</td>
</tr>
<tr>
<td>Qfy</td>
<td>Intermittently active fluvial fine-grained alluvium</td>
<td>Late Holocene</td>
<td>Brown to gray sand, silt, mud, and interbedded gravel.</td>
</tr>
<tr>
<td>Qscd</td>
<td>Intermediate fine-grained deposits associated with past ground-water discharge</td>
<td>Late Pleistocene</td>
<td>Top 1-2 m is characteristically resistant light-gray calcareous mud that is partially cemented with calcite</td>
</tr>
<tr>
<td>Qsu</td>
<td>Undivided young and intermediate fine-grained deposits associated with past ground-water discharge</td>
<td>Early Holocene and late Pleistocene</td>
<td>Light-gray to light-brown unconsolidated silt, sandy silt, silty sand, and mud or the top 1-2 m is characteristically resistant light-gray calcareous mud that is partially cemented with calcite</td>
</tr>
</tbody>
</table>

*Unit= map unit
Figure 4.1. Results of post-hoc comparisons of mean plot volume and density by soil map unit using the Tukey-Kramer test. Graphs show means and standard errors. Different letters represent significant differences at \( P < 0.05 \). Means and standard errors were back-transformed from cube root transformed estimates. Soil abbreviations: AR = Arizo; BL = Badland; DM = Dalian-McCullough Complex; LD = Las Vegas-DeStazo Complex; LV = Las Vegas; WE = Weiser; WW = Weiser-Wechech Association.
Figure 4.2. Results of post-hoc comparisons of mean plot volume and density by geologic type using the Tukey-Kramer test. Graphs show means and standard errors. Different letters represent significant differences at $P < 0.05$. Graphs without letters indicate no significant differences. Means and standard errors were back-transformed from cube root transformed estimates. Geology abbreviations: QI = Qai; QY = Qay; QO = Qayo; YY = Qayy, QF = Qfy; QD = Qscd; QU = Qsu.
Figure 4.3. Results of post-hoc comparisons of mean plot volume and density by vegetation association using the Tukey-Kramer test. Graphs show means and standard errors. Different letters represent significant differences at $P < 0.05$. Graphs without letters indicate no significant differences. Means and standard errors were back-transformed from cube root transformed estimates. Vegetation abbreviations: AD = *Ambrosia dumosa* - *Atriplex confertifolia* Association; AU = *Ambrosia dumosa* - *Larrea tridentata* Upper Alluvial Fan Association; AM = *Ambrosia dumosa* - *Menodora spinescens* Association; AP = *Atriplex polycarpa* - *Ambrosia dumosa* Association, BL = Badlands; LT = *Larrea tridentata* Association; LA = *Larrea tridentata* - *Ambrosia dumosa* Association.
Figure 4.4. OLS regression results showing the log-log plots of total plot volume vs. plot density. Plots are for all species sampled on the ULVWCTA ($F_{(1,222)} = 64.13, P < .0001, R^2 = 0.221$), for all *Larrea tridentata* shrubs sampled on the ULVWCTA $F_{(1,201)} = 156.7, P < .0001, R^2 = 0.435$), and for all *Ambrosia dumosa* shrubs sampled on the ULVWCTA ($F_{(1,182)} = 419.1, P < .0001$). Results are significant at $P < 0.05$. 

*All species*

![Log-log plot for all species](image1)

*Larrea tridentata*

![Log-log plot for Larrea tridentata](image2)

*Ambrosia dumosa*

![Log-log plot for Ambrosia dumosa](image3)
Figure 4.5. OLS regression results showing the log-log plots of mean plot volume vs. plot density. Plots are for all species sampled on the ULVWCTA ($F_{(1,222)} = 3.509, P = 0.062, R^2 = 0.011$), for all *Larrea tridentata* shrubs sampled on the ULVWCTA ($F_{(1,201)} = 0.00002, P = 0.996, R^2 = -0.005$), and for all *Ambrosia dumosa* shrubs sampled on the ULVWCTA ($F_{(1,182)} = 7.48, P = 0.007, R^2 = 0.034$). Results are significant at $P < 0.05$. 
CHAPTER 5
SUMMARY

Ecological communities are complex, the structure of which equals the sum of the interactions between community characteristics and the abiotic and biotic factors shaping them. Because of this complexity, communities are often studied in their component parts, giving special focus to one or two aspects of community structure. While this might be the most practical method to study communities, this approach often neglects other characteristics that, with their inclusion, would paint a more complete picture of community ecology.

The studies described in this dissertation were conducted in an effort to synthesize the complexity that is inherent in ecological communities. Following Tillman’s (1982) list of characteristics describing community structure (species composition, abundance, diversity, the spatial and temporal patterning of species abundances, and morphological characteristics of the dominant species), we designed this dissertation to address each characteristic so as to gain a more complete understanding of the plant communities inhabiting the ULVWCTA. While the individual studies follow traditional methodology and break communities into their component parts, each study was designed to address a separate component of community structure, which, taken as a whole, would provide more well-defined account of arid plant community structure.

Specifically, Chapter 2 examined the abiotic influences on species composition, abundance, and diversity for each plant community on the ULVWCTA. While it is known that soil, geology, topography, and bioclimatic factors influence arid plant
communities, the relative contribution of these factors has remained unclear. This study confirmed the overall importance of substrate properties (i.e. soil map unit and geologic unit) on plant community structure. Subtle differences in substrate texture and age may lead to large differences in plant available water.

Knowing that substrate and climate and their influence on potential water availability appear to direct species composition and abundance for plant communities on the ULVWCTA, Chapters 3 and 4 focused on the interplay between soil and geologic variables and other aspects of community structure. Chapter 3 investigated the biotic influences within each plant community on the ULVWCTA. While numerous studies have analyzed dispersion patterns as a means to generate hypotheses regarding the biotic influences on community structure, most were limited to one or several species or did not incorporate substrate as an important control factor. Our study was novel in that it compared dispersion patterns between entire plant communities growing on different substrates. Our results indicate that random and clumping patterns occur more often than uniform spatial patterns, indicating that facilitation may be the predominant plant-plant interaction on this site. We also saw dispersion patterns change between soils and geologic substrates of different textures and ages, demonstrating the strong influence of substrate in shaping plant-plant interactions in arid environments.

Chapter 4 examined patterns of size and abundance within and among plant communities growing on different substrates across the ULVWCTA and also investigated the self-thinning relationship and its applicability in this arid environment. There have been conflicting results in the few studies have investigated the role of self-thinning in
arid environments, with some observing a self-thinning relationship and others citing a weak relationship. Overall, we saw plant size and abundance patterns change significantly between soil map units, geologic units, and plant community associations. In addition, our results did not provide evidence of self-thinning relationships, but instead showed significant positive relationships in the log-log plots of plot density vs. total plot volume for all species together, for *L. tridentata* alone, and *A. dumosa* alone. Our results support the strong role of substrate variables in determining plant community structure as well as theories predicting that facilitation is a dominant component in arid plant communities.

By addressing multiple aspects of community structure in addition to both the abiotic and biotic variables influencing these characteristics, we have been afforded a more complete understanding of plant community dynamics on the ULVWCTA. Taken as a unit, each study provides support for the others. Overall, each study emphasized the importance of substrate variables and their role in shaping plant community structure on the ULVWCTA. Future studies should provide this same emphasis, addressing plant communities and the underlying substrate as a unit, whether for research or management purposes. In addition, Chapters 3 and 4 provide evidence of the strong role that facilitation plays on this site and possibly arid plant communities as a whole. Ecologists have long debated the roles of competition and facilitation in arid environments and should consider a multifaceted approach like the one described here to gain perspective to these long standing questions.
Our approach, while not simple, is important for community ecology as a science. It is difficult to understand community structure using only smaller, fragmented studies. The comprehensive approach described here will enable ecologists to gain a more complete understanding of community dynamics and apply this knowledge to various climate change and land management scenarios. This is particularly important for arid and semi-arid environments which cover approximately one third of the earth’s land area may be some of the most sensitive to climate change (Maestre et al. 2005). In addition, there is a growing need for large ecological assessments which provide datasets such as the one described here. These large datasets provide the opportunity for more comprehensive community studies.

Despite the need for more holistic community studies, this dissertation has revealed a large disconnect between theoretical, mathematical, and applied ecology, one that could impede progress for practical purposes. Essentially, the smaller areas of study that make up current community ecology are individual topics in ecology in their own right, each with a rich and complicated history of theory and methodology. Essentially, each chapter of this dissertation could have been a stand-alone research topic. It was challenging to combine these topics and understand the intricacies in the background literature and statistical approaches. As such, most of the statistical methods presented are not practical for an applied ecologist, land manager, or ecological consultant needing to manage and inventory ecological communities and make on the ground decisions. In summary, community ecology is in need of a more collaborative and multidisciplinary
approach in addition to developing practical methodology for field ecologists that goes beyond simple maps and basic descriptions.

LITERATURE CITED


Appendix A. Woody perennial species identified in the ULVWCTA.

Names and authorities follow those used by the USDA (http://plants.usda.gov). Names do not necessarily follow those of general usage.

AGAVACEAE  – Agave Family


ASTERACEAE  – Sunflower Family


**BRASSICACEAE – Mustard Family**


**CACTACEAE – Cactus Family**


*Cylindropuntia ramosissima* (Engelm.) F.M. Knuth. Branched pencil cholla. Shrub. (CYLRAM)


**CHENOPODIACEAE – Goosefoot Family**


**EPHEDRAECEAE - Ephedra Family**


*Ephedra torreyana* S. Watson. Torrey's jointfir. Shrub/subshrub. (EPHTOR)
FABACEAE - Pea Family

*Acacia greggii* A. Gray.  Catclaw acacia.  Tree/shrub.  (ACAGRE).


KRAMERIACEAE – Krameria Family


OLEACEAE – Olive Family

*Menodora spinescens* A. Gray.  Spiny menodora.  Shrub.  (MENSPI)

ONAGRACEAE - EVENING PRIMROSE FAMILY


POLYGONACEAE – Buckwheat Family


RUTACEAE – Rue Family


SOLANACEAE – Nightshade Family


*Lycium* L.  Desert-thorn.  (LYCSPP).
ZYGO PHYLLACEAE – Caltrop Family

Appendix B. Plots with corresponding elevation, vegetation associations, soil map units, and geologic units.

Table B.1. Plots with elevation, vegetation associations, soil types, and geologic units.

<table>
<thead>
<tr>
<th>Plot Number</th>
<th>Elevation (m)</th>
<th>Vegetation Association</th>
<th>Soil Map Unit</th>
<th>Geologic Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2879</td>
<td><em>Larrea tridentata</em> - <em>Ambrosia dumosa</em> Association</td>
<td>Weiser-Wechech Association</td>
<td>Qayo</td>
</tr>
<tr>
<td>2</td>
<td>2912</td>
<td><em>Larrea tridentata</em> - <em>Ambrosia dumosa</em> Association</td>
<td>Weiser-Wechech Association</td>
<td>Qayo</td>
</tr>
<tr>
<td>3</td>
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<td>6</td>
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<td>Weiser-Wechech Association</td>
<td>Qay</td>
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<td>Qay</td>
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</tbody>
</table>

(Continued on next page)
Table B.1. Plots with elevation, vegetation associations, soil map units, and geologic units (continued).

<table>
<thead>
<tr>
<th>Plot Number</th>
<th>Elevation (m)</th>
<th>Vegetation Association</th>
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<th>Geologic Unit</th>
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Table B.1. Plots with elevation, vegetation associations, soil map units, and geologic units (continued).

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Table B.1. Plots with elevation, vegetation associations, soil map units, and geologic units (continued).

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Table B.1. Plots with elevation, vegetation associations, soil map units, and geologic units (continued).

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Table B.1. Plots with elevation, vegetation associations, soil map units, and geologic units (continued).

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Table B.1. Plots with elevation, vegetation associations, soil map units, and geologic units (continued).

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Table B.1. Plots with elevation, vegetation associations, soil map unit, and geologic units (continued).

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Table B.1. Plots with elevation, vegetation associations, soil map units, and geologic units (continued).

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Table B.1. Plots with elevation, vegetation associations, soil map units, and geologic units (continued).

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Appendix C. Species found within each survey plot
(Species abbreviations can be found in Appendix A)

Table C.1. Plot, species, number of occurrences, and sum of cover

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Table C.1. Plot, species, number of occurrences, and sum of cover (continued).

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Table C.1. Plot, species, number of occurrences, and sum of cover (continued).

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Table C.1. Plot, species, number of occurrences, and sum of cover (continued).

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Appendix D. Scree plot of NMDS dimensions vs. stress values

Figure D.1. Scree plot depicting NMDS stress value for analyses run in one, two, three, four, five, and six dimensions. Stress values were determined after 500 iterations.
Appendix E. NMDS ordination results

Figure E.1. Ordination diagram of NMDS axes one and two with geology variables. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = *Ambrosia dumosa*; atrcon = *Atriplex confertifolia*; atrpol = *Atriplex polycarpa*; cylech = *Cylindropuntia echinocarpa*; encvir = *Encelia virginensis*; ephnev = *Ephedra nevadensis*; ephtor = *Ephedra torreyana*; gutspp = *Gutierrezia species*; hymsal = *Hymenolea salsola*; kraere = *Krameria erecta*; latri = *Larrea tridentata*; lycand = *Lycium andersonii*; menspi = *Menodora spinescens*; opubas = *Opuntia basilaris*; psofre = *Psorothamnus fremontii*; xyltor = *Xylorhiza tortifolia*; yucs = *Yucca schidigera*.
Figure E.2. Ordination diagram of NMDS axes one and two with soil variables. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = *Ambrosia dumosa*; atrcon = *Atriplex conferta*; atrpol = *Atriplex polycarpa*; cylech = *Cylindropuntia echinocarpa*; encvir = *Encelia virginensis*; ephnev = *Ephedra nevadensis*; ephtor = *Ephedra torreyana*; gutspp = *Gutierrezia species*; hymsal = *Hymenoclea salsola*; kraer = *Krameria erecta*; latri = *Larrea tridentata*; lyca = *Lycium andersonii*; menspi = *Menodora spinescens*; opubas = *Opuntia basilaris*; psofre = *Psorothamnus fremontii*; xyltor = *Xylorhiza tortifolia*; yucsch = *Yucca schidigera*
Figure E.3. Ordination diagram of NMDS axes one and two with vegetation association variables. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = Ambrosia dumosa; atrcon = Atriplex confertifolia; atrpol = Atriplex polycarpa; cylech = Cylindropuntia echinocarpa; encvir = Encelia virginensis; ephnev = Ephedra nevadensis; ephtor = Ephedra torreyana; gutspp = Gutierrezia species; hymsal = Hymenoclea salsola; kraere = Krameria erecta; latri = Larrea tridentata; lycand = Lycium andersonii; menspi = Menodora spinescens; opubas = Opuntia basilaris; psoref = Psorothamnus fremontii; xyltor = Xylorhiza tortifolia; yucsch = Yucca schidigera
Figure E.4. Ordination diagram of NMDS axes one and three with geology variables. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = Ambrosia dumosa; atrcon = Atriplex confertifolia; atrpol = Atriplex polycarpa; cylech = Cylindropuntia echinocarpa; encvir = Encelia virginensis; epheve = Ephedra nevadensis; ephtor = Ephedra torreyana; gutspp = Gutierrezia species; hynsal = Hymenoclea salsola; kraere = Krameria erecta; latri = Larrea tridentata; lycand = Lycium andersonii; menspi = Menodora spinescens; opubas = Opuntia basilaris; psotre = Psorothamnus fremontii; xyltor = Xylorhiza tortifolia; yucsch = Yucca schidigera.
Figure E.5. Ordination diagram of NMDS axes one and three with soil variables. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = *Ambrosia dumosa*; atrcon = *Atriplex confertifolia*; atrpol = *Atriplex polycarpa*; cylech = *Cylindropuntia echinocarpa*; encvir = *Encelia virginensis*; ephnev = *Ephedra nevadensis*; ephtor = *Ephedra torreyana*; gutpp = *Gutierrezia* species; hynsal = *Hymenoclea salsa*; kraere = *Krameria erecta*; latri = *Larrea tridentata*; lycand = *Lycium andersonii*; menspi = *Menodora spinescens*; opubas = *Opuntia basilaris*; psorf = *Psorothamnus fremontii*; xyltor = *Xylorhiza tortifolia*; yucsch = *Yucca schidigera*
Figure E.6. Ordination diagram of NMDS axes one and three with vegetation association variables. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = Ambrosia dumosa; atrcon = Atriplex confertifolia; atropol = Atriplex polycarpa; cylech = Cylindropuntia echinocarpa; encvir = Encelia virginensis; ephnve = Ephedra nevadensis; ephtor = Ephedra torreyana; gutspp = Gutierrezia species; hymsal = Hymenoclea salsola; kraere = Krameria erecta; latri = Larrea tridentata; lycand = Lycium andersonii; menspi = Menodora spinescens; opubas = Opuntia basilaris; psorfre = Psorothamnus fremontii; xyltor = Xylorhiza tortifolia; yucsch = Yucca schidigera
Figure E.7. Ordination diagram of NMDS axes two and three with geology variables. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = Ambrosia dumosa; atrcon = Atriplex confertifolia; atrpol = Atriplex polycarpa; cylech = Cylindropuntia echinoarpa; enevir = Encelia virginensis; ephnev = Ephedra nevadensis; ephtor = Ephedra torreyana; gutspp = Gutierrezia species; hymsal = Hymenoclea salsoila; kraere = Krameria erecta; latri = Larrea tridentata; lycand = Lycium andersonii; menspi = Menodora spinescens; opubas = Opuntia basilaris; psofre = Psorothamnus fremontii; xyltor = Xylorhiza tortifolia; yucsch = Yucca schidigera.
Figure E.8. Ordination diagram of NMDS axes one and three with soil variables. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = *Ambrosia dumosa*; atrcon = *Atriplex confertifolia*; atrpol = *Atriplex polycarpa*; cylech = *Cylindropuntia echinocarpa*; encvir = *Encelia virginensis*; ephnev = *Ephedra nevadensis*; ephtor = *Ephedra torreyana*; gutspp = *Gutierrezia species*; hymsal = *Hymenoclea salsola*; kraere = *Krameria erecta*; latri = *Larrea tridentata*; lycand = *Lycium andersonii*; menspi = *Menodora spinescens*; opubas = *Opuntia basilaris*; psofre = *Psorothamnus fremontii*; xyltor = *Xylorhiza tortifolia*; yucs = *Yucca schidigera*. 
Figure E.9. Ordination diagram of NMDS axes two and three with vegetation association variables. The diagram arranges variables such that the distance between points corresponds with the dissimilarity between variables. Larger distances are most accurate. Species abbreviations: ambdum = *Ambrosia dumosa*; atrcon = *Atriplex confertifolia*; atrpol = *Atriplex polycarpa*; cylech = *Cylindropuntia echinocarpa*; encvir = *Encelia virginensis*; ephnve = *Ephedra nevadensis*; ephtor = *Ephedra torreyana*; gutspp = *Gutierrezia species*; hymsal = *Hymenolea salsola*; kraere = *Krameria erecta*; latri = *Larrea tridentata*; lycand = *Lycium andersonii*; menspi = *Menodora spinescens*; opubas = *Opuntia basilaris*; psofre = *Psorothamnus fremontii*; xyltor = *Xylorhiza tortifolia*; yuchsch = *Yucca schidigera*
Table E.1. NMDS plot scores by axis.

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Table E.1. NMDS plot scores by axis (continued).

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Table F.1. CCA plot scores by axis (continued)

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Appendix G. Transect plots with corresponding elevation, vegetation associations, soil types, and geologic units.

Table G.1. Transect plots with corresponding elevation, vegetation associations, soil types, and geologic units. Transect 1 = T1 and Transect 2 = T2.

<table>
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<th>Plot</th>
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<th>Vegetation Association</th>
<th>Soil Type</th>
<th>Geologic Unit</th>
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<td>Qay</td>
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(Continued on next page)
Table G.1. Transect plots with corresponding elevation, vegetation associations, soil types, and geologic units. Transect 1 = T1 and Transect 2 = T2 (continued).

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<th>Geologic Unit</th>
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Appendix H. Species found within each transect survey plot  
(Species abbreviations can be found in Appendix A)

Table H.1. Plot, species, and number of occurrences for Transect 1 (T1) and Transect 2 (T2).

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Table H.1. Plot, species, and number of occurrences for Transect 1 (T1) and Transect 2 (T2) (continued).

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Table H.1. Plot, species, and number of occurrences for Transect 1 (T1) and Transect 2 (T2) (continued).

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Table H.1. Plot, species, and number of occurrences for Transect 1 (T1) and Transect 2 (T2) (continued).

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Appendix I. L-function plots

Plot I.1. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 1 (T1) Plot 1. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes (\(N_{sim}=199\)). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{ in meters})\) over which the pattern was tested.
Plot I.2. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 1 (T1) Plot 2. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{ in meters})\) over which the pattern was tested.
Plot I.3. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 1 (T1) Plot 3. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{in meters})\) over which the pattern was tested.
Plot I.4. L-function plots for all species and *L. tridentata* alone in Transect 1 (T1) Plot 4. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{ in meters})\) over which the pattern was tested.
Plot I.5. L-function plots for all species and *L. tridentata* alone in Transect 1 (T1) Plot 5. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{ in meters})\) over which the pattern was tested.
Plot I.6. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 1 (T1) Plot 6. Solid lines represent the estimated L-statistic plotted as \( (L(t) - t) \). Shaded areas represent the Monte Carlo simulation envelopes (\( N_{sim}=199 \)). Values of \( (L(r) - t) \) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \( (t, \text{in meters}) \) over which the pattern was tested.
Plot I.7. L-function plots for all species and *L. tridentata* alone in Transect 1 (T1) Plot 7. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{\text{sim}}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{ in meters})\) over which the pattern was tested.
Plot I.8. L-function plots for all species and *L. tridentata* alone in Transect 1 (T1) Plot 8. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{ in meters})\) over which the pattern was tested.
Plot I.9. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 1 (T1) Plot 9. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{ in meters})\) over which the pattern was tested.
Plot I.10. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 1 (T1) Plot 10. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{in meters})\) over which the pattern was tested.
Plot 1.11. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 1 (T1) Plot 11. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{\text{sim}}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{ in meters})\) over which the pattern was tested.
Plot I.12. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 1 (T1) Plot 12. Solid lines represent the estimated L-statistic plotted as \( L(t) - t \). Shaded areas represent the Monte Carlo simulation envelopes \( (N_{sim}=199) \). Values of \( L(r) - t \) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \( (t, \text{in meters}) \) over which the pattern was tested.
Plot I.13. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 1 (T1) Plot 13. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{in meters})\) over which the pattern was tested.
Plot I.14. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 2 (T2) Plot 1. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(t) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{in meters})\) over which the pattern was tested.
Plot I.15. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 2 (T2) Plot 2. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{in meters})\) over which the pattern was tested.
Plot I.16. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 2 (T2) Plot 3. Solid lines represent the estimated L-statistic plotted as *(L(t) - t)*. Shaded areas represent the Monte Carlo simulation envelopes *(N_{sim}=199)*. Values of *(L(t) - t)* greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale *(t, in meters)* over which the pattern was tested.
Plot I.17. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 2 (T2) Plot 4. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{ in meters})\) over which the pattern was tested.
Plot I.18. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 2 (T2) Plot 5. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{in meters})\) over which the pattern was tested.
Plot I.19. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 2 (T2) Plot 6. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{in meters})\) over which the pattern was tested.
Plot I.20. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 2 (T2) Plot 7. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes (\(N_{sim}=199\)). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{ in meters})\) over which the pattern was tested.
Plot I.21. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 2 (T2) Plot 8. Solid lines represent the estimated L-statistic plotted as \( L(t) - t \). Shaded areas represent the Monte Carlo simulation envelopes \( (N_{sim} = 199) \). Values of \( L(r) - t \) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \( (t, \text{ in meters}) \) over which the pattern was tested.
Plot I.22. L-function plots for all species, *Ambrosia dumosa* alone, and *Larrea tridentata* alone in Transect 2 (T2) Plot 9. Solid lines represent the estimated L-statistic plotted as $(L(t) - t)$. Shaded areas represent the Monte Carlo simulation envelopes ($N_{sim}=199$). Values of $(L(r) - t)$ greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale (t, in meters) over which the pattern was tested.
Plot I.23. L-function plots for all species, *A. dumosa* alone, and *L. tridentata* alone in Transect 2 (T2) Plot 10. Solid lines represent the estimated L-statistic plotted as \((L(t) - t)\). Shaded areas represent the Monte Carlo simulation envelopes \((N_{sim}=199)\). Values of \((L(r) - t)\) greater than the upper simulation envelope indicate significant clumping relative to the null hypothesis of complete spatial randomness, while values less than the lower simulation envelope indicate significant uniformity. Horizontal axis values represent the scale \((t, \text{ in meters})\) over which the pattern was tested.
CURRICULUM VITAE

Amy A. Croft
260 N. 400 E.
Providence, Utah 84332
435-757-1511
amy.a.croft@gmail.com

EDUCATION

2016  Ph.D. Ecology/Biology, Utah State University, Logan, Utah
2016  National Environmental Policy Act (NEPA) Certificate Program
2003  M.S. Plant Science, Utah State University, Logan, Utah
1999  B.S. Biology, Utah State University, Logan, Utah

BIOLOGICAL RESEARCH AND PROFESSIONAL EXPERIENCE

- Serves as a member of the research and development team for Baicor, L.C., a specialty fertilizer company that manufactures products for home and garden, agriculture, greenhouse growers, golf, and private label. Manages all aspects of greenhouse experiments and data analysis. Maintains laboratory chemical inventory and develops QA/QC record keeping systems. Administers the production of official product Safety Data Sheets using MSDgen hazard communication and chemical regulatory compliance software. Collaborates with an interdisciplinary team of scientists and business professionals in the research and development of a novel fungicide, a project funded by the National Science Foundation.

Utah State University, Department of Biology, Logan, UT, Graduate Student.  Dr. Jim MacMahon, Major Professor (2006-2016).
- Dissertation research explored the influence of abiotic (soil, geology, and climate variables) and biotic (plant-plant interactions) variables in shaping multiple aspects of plant community structure in a Mojave Desert ecosystem. Designed data collection methods to inventory vegetation stands across 7,400 hectares of BLM land. Managed and analyzed a large scale database complete with plant, soil, climate, and GIS data. Used complex multivariate and spatial techniques for statistical analysis of vegetation, soil, and climate data. Supervised field crews and maintained working relationships with BLM professionals as well as an interdisciplinary team of academic scientists.

- California False Hellebore Population Assessment.  Blaise Chanson, Supervisor (2009-2012). Managed teams to locate populations of Veratrum californicum (California false hellebore) in alpine habitats throughout Utah and Idaho. Work was performed for Infinity Pharmaceuticals, Inc., a company interested in investigating the plant for its potential antitumor properties. Directed team field work responsibilities and coordinated agency and private property communication. Oversaw database
management and QA/QC. Performed general statistical analysis and predictive habitat modeling. Organized technical reports and conference presentations.

- **Ash Meadows Wildlife Refuge Rare and Endemic Plant Surveys.** Alyson Eddie, Supervisor (2010). Provided statistical analysis and predictive habitat models to delineate potential critical habitat areas for 12 sensitive and rare plant species on the Refuge. The models were used in an effort to understand species distribution and aid in habitat management plans.

- **Lower Colorado River Multi-Species Conservation Program Vegetation Monitoring Study.** Alyson Eddie, Supervisor (2009). Provided statistical analysis and summary of data for a long-term vegetation monitoring program. The objective of the study was to assist the U.S. Bureau of Reclamation, Lower Colorado Region, with long-term management decisions pertaining to the success of habitat creation areas.


**USU Archeological Services, Logan, UT, Ecologist.** Dr. Ken Cannon, Supervisor (2010).

- **Environmental Assessment (EA) for the Wyoming Loop Completion Projects.** Conducted field surveys and prepared the soils and geology components of the Environmental Assessment needed for the installation of 100 miles+/- of high-capacity broadband fiber optic cable in the Greater Yellowstone area (Teton County, Wyoming). EA prepared for the National Telecommunications & Information Administration Broadband Technology Opportunities Program, Washington, DC.

**Utah State University, Logan, UT, Research Assistant.** Dr. Jim MacMahon, Supervisor (2006-2009).

- Worked as part of an interdisciplinary team of scientists investigating sensitive plant, fossil, and soil resources for the Upper Las Vegas Wash Conservation Transfer Area, a 7,400 hectare land parcel of Mojave Desert. Oversaw extensive vegetation surveys and managed a large scale database complete with plants, soil, and GIS data. Assisted in soil classification and the preparation of vegetation and soil maps for the area. Collaborated in the development of predictive habitat models for two sensitive and rare plant species, *Arctomecon californica* (California bearpoppy) and *Eriogonum corymbosum* var. *nilesii* (Las Vegas buckwheat). Assessed the magnitude of disturbance from off-road vehicles and trash and assisted in the development of alternative futures scenarios for the site.

**Balance Environmental, Logan, UT, Ecologist.** Nate Norman, Supervisor (2008-2009).

- **Bateman and Hall Construction Water-Quality Sampling and Wetland Monitoring.** Duties included coordination with property owners and collection of water samples and stream flow measurements to ensure construction activities followed environmental guidelines to ensure riparian health. Reports were written summarizing and analyzing results for each month of operation.

- **Salt Lake City 16-inch Pipeline (AREPI) Construction Monitoring.** Duties included monitoring the contractor's activities during construction to verify compliance with environmental permits and specifications. Nate Norman, Supervisor (2008).
Utah Botanical Center, Utah State University, Logan, UT, Research Associate. Bill Varga, Supervisor (2003-2006).

- Managed the design and installation of pot-in-pot nursery. Technical lead for the native Plant Trialing Program which focused on propagation and seed selection research for plants native to the Intermountain West. Supported the Native Seed Increase Project by collecting seed and establishing native plant stock blocks. Organized statewide seed scouting and voucher specimen collection trips. Managed multiple greenhouse spaces used for native plant propagation. Public education of water-wise landscaping principles and representation at academic and Green Industry conferences. Special event planning as well as book, letter, and grant writing.

Utah State University, Logan, UT, Graduate Student. Dr. Roger Kjelgren, Major Professor (2000-2003).

- Thesis research focused on the development of a pot-in-pot nursery production system and its effects on the growth of native and drought adapted plants for the Intermountain West. Monitored plant growth within the production system to determine the nursery and landscape potential of each plant species as well as the overall economic potential of the system.

Fisheries Experiment Station, Logan, UT, Research Associate. Eric Wagner, Supervisor (1999).

- Studied viability of the Whirling Disease parasite; performed salinity tests to determine levels at which the parasite could survive.

Utah State University, Logan, UT, Undergraduate Research Assistant. (1996-2000)


- Dyers Woad Population Control Project. Dr. Dane Hansen, Supervisor (1997, 1998, 2000). Identified and collected rust infected Dyers Woad (*Isatis tinctoria*); measured and marked growing weeds; counted germinating rust spores; assisted with biological control experiments.

- Utah Water Research Laboratory. Joan McLean, Supervisor (1996). Collected and tested pH of leachate water samples from birch trees and Carex grasses growing in lead contaminated soils; general laboratory maintenance and care.

OTHER SKILLS

- Proficiency with Microsoft Office programs.
- Experience programming in R and SAS statistical programs.
- Completed short course on predictive habitat modeling, Utah State University, 2010.
• Completed NEPA courses (taught by the Shipley Group, 2010-2011): How to Manage the NEPA Process and Write Effective NEPA Documents, Clear Writing for NEPA Specialists, Reviewing NEPA Documents, Cultural and Natural Resource Management, Cumulative Impacts Analysis and Documentation, Overview of the Endangered Species Act, and NEPA Climate Change Analysis.
• Experience applying herbicides, pesticides, and fungicides.
• Experience operating off-road vehicles over variable terrain and conditions.
• Experience using radio telemetry and GPS equipment.

POSTERS


INVITED TALKS
March 2009, 5th Southwest Rare Plant Conference, Changing Landscapes in the Southwest.

TECHNICAL PUBLICATIONS


TEACHING EXPERIENCE

- **Biology and the Citizen, Teaching Assistant**, Biology 1010, Utah State University (Spring 2010)
- **Plant Physiology Laboratory**, Biology 4400, Utah State University (Fall 2008, 2009, 2010)
- **Human Physiology Laboratory**, Biology 2420, Utah State University (Summer 2009)
- **General Biology Laboratory**, Biology 1620, Utah State University (Spring 2009, Spring 2011, Spring 2012).

AWARDS

- PhD Assistantship, Ecology Center, Utah State University, 2011-2012.
- Teaching Assistantship, Department of Biology, Utah State University, 2008-2012.
- Research Assistantship, Department of Biology, Utah State University, 2006-2008.
- Research Assistantship, Department of Plants, Soils, and Biometeorology, Utah State University, 2001-2003.