

December 2015

## Assessing the importance of nurse plant associations to the growth of pre-reproductive *Yucca brevifolia*

Eric James Chameroy  
University of Nevada, Las Vegas, [chameroy@unlv.nevada.edu](mailto:chameroy@unlv.nevada.edu)

Follow this and additional works at: <https://digitalscholarship.unlv.edu/thesesdissertations>



Part of the [Biology Commons](#), [Botany Commons](#), [Environmental Sciences Commons](#), and the [Terrestrial and Aquatic Ecology Commons](#)

---

### Repository Citation

Chameroy, Eric James, "Assessing the importance of nurse plant associations to the growth of pre-reproductive *Yucca brevifolia*" (2015). *UNLV Theses, Dissertations, Professional Papers, and Capstones*. 2524.

<https://digitalscholarship.unlv.edu/thesesdissertations/2524>

This Thesis is protected by copyright and/or related rights. It has been brought to you by Digital Scholarship@UNLV with permission from the rights-holder(s). You are free to use this Thesis in any way that is permitted by the copyright and related rights legislation that applies to your use. For other uses you need to obtain permission from the rights-holder(s) directly, unless additional rights are indicated by a Creative Commons license in the record and/or on the work itself.

This Thesis has been accepted for inclusion in UNLV Theses, Dissertations, Professional Papers, and Capstones by an authorized administrator of Digital Scholarship@UNLV. For more information, please contact [digitalscholarship@unlv.edu](mailto:digitalscholarship@unlv.edu).

ASSESSING THE IMPORTANCE OF NURSE PLANT ASSOCIATIONS TO THE GROWTH  
OF PRE-REPRODUCTIVE *YUCCA BREVIFOLIA*

By

Eric James Chameroy

Bachelor of Science – Ecology and Evolutionary Biology

University of Connecticut

1999

A thesis submitted in partial fulfillment

of the requirements for the

Master of Science – Biological Sciences

School of Life Sciences

College of Sciences

The Graduate College

University of Nevada, Las Vegas

December 2015

**Thesis Approval**

The Graduate College  
The University of Nevada, Las Vegas

November 9, 2015

This thesis prepared by

Eric Chameroy

entitled

Assessing the Importance of Nurse Plant Associations to the Growth of Pre-Reproductive  
*Yucca brevifolia*

is approved in partial fulfillment of the requirements for the degree of

Master of Science – Biological Sciences  
Department of Life Sciences

Lawrence R. Walker, Ph.D.  
*Examination Committee Chair*

Kathryn Hausbeck Korgan, Ph.D.  
*Graduate College Interim Dean*

Todd C. Esque, Ph.D.  
*Examination Committee Member*

Lloyd R. Stark, Ph.D.  
*Examination Committee Member*

Daniel B. Thompson, Ph.D.  
*Examination Committee Member*

Stephen M. Rowland, Ph.D.  
*Graduate College Faculty Representative*

ABSTRACT

**Assessing the Importance of Nurse Plant Associations  
to the Growth of Pre-Reproductive  
*Yucca brevifolia***

by

Eric James Chameroy

Dr. Lawrence R. Walker, Examination Committee Chair  
Professor of Biological Sciences  
University of Nevada, Las Vegas

Facilitation and competition among plant species, in addition to abiotic factors, play an important role in determining plant community structure in arid and semi-arid environments. I conducted a study in Dry Lake Valley, Lincoln County, Nevada, USA to investigate the importance of nurse plant associations to pre-reproductive *Yucca brevifolia* (Joshua tree). Dry Lake Valley lies within a transition desert between the Mojave and Great Basin Deserts with ecotonal plant communities consisting of species representative of both deserts. A vegetation survey described the communities in which this study was conducted as a *Y. brevifolia* woodland dominated by an understory of *Ephedra nevadensis* (mormon tea) and *Grayia spinosa* (spiny hopsage). Pairings of adult *G. spinosa* and pre-reproductive *Y. brevifolia* were selected as part of a removal field experiment to determine whether interactions between these species were facilitative or competitive and if continued growth of *Y. brevifolia* would result in the eventual exclusion of *G. spinosa*. Another survey investigated whether desert shrubs provide pre-reproductive *Y. brevifolia* protection from herbivores through associational resistance. Results did not indicate the occurrence of direct competition or facilitation between *Y. brevifolia* and *G. spinosa*. However, there was evidence that *Y. brevifolia* experience reduced herbivory damage by growing in proximity to desert

shrubs. This study demonstrated that pre-reproductive *Y. brevifolia* are indirectly facilitated by nurse plants through associational resistance. This study also demonstrated the need to better understand the ontogeny of *Y. brevifolia* as it relates to soil niche development, and in turn, its interactions with its benefactor species.

## ACKNOWLEDGEMENTS

First and foremost, I give my sincerest thanks to my advisor, Dr. Lawrence Walker, for his willingness to take me under his wing. Through his patience, understanding, and wisdom, I have been able to successfully navigate the arduous ordeal that is called “graduate school”. I also thank him for showing me many of the wonders of the Mojave Desert. I also thank the rest of my graduate committee: Dr. Todd Esque (USGS), Dr. Daniel Thompson, Dr. Lloyd Stark, and Dr. Steve Rowland (Department of Geoscience).

I thank the Bureau of Land Management (Caliente Field Office) for granting me the permit to allow me to conduct this project and to the UNLV Graduate and Professional Student Association for providing me with the funding necessary to carry out nutrient analysis.

I extend my thanks to Dr. Leslie DeFalco (USGS). My return to graduate school certainly had many bumps and I was feeling quite stressed and unsure of myself entering into my initial field season. I am grateful for her taking the time to talk me away from the proverbial edge of the cliff.

There's no way I could have completed all of the field work required for this project without my small army of helpers. Laine Adame, Robert Dostler, Jasminn Gray, and Gurpal Singh – I am grateful for all of their help. Especially Rob, who was a workhorse in the field! I also thank Felicia Chen (USGS), Tim Duffey (UNLV), and Fred Landau (UNLV) for their contributions.

I also cannot forget my favorite field assistant, my wife Miki, who accompanied me on many field excursions because she hated seeing me go out alone and wanted to catch glimpses of jackrabbits, cottontails, and (maybe) desert tortoises. I couldn't have done any of this without her love and support.

TABLE OF CONTENTS

ABSTRACT..... iii

ACKNOWLEDGEMENTS .....v

LIST OF TABLES ..... viii

LIST OF FIGURES ..... ix

CHAPTER 1: INTRODUCTION.....1

    Purpose of Study .....5

    Study Location .....7

CHAPTER 2: DESCRIPTION OF THE PLANT COMMUNITIES OF DRY LAKE VALLEY, LINCOLN COUNTY, NEVADA, USA.....9

    Introduction.....9

    Materials and Methods .....11

    Results.....12

    Discussion.....14

CHAPTER 3: COMPETITIVE AND FACILITATIVE INTERACTIONS BETWEEN *YUCCA BREVIFOLIA* AND *GRAYIA SPINOSA* IN NURSE PLANT PAIRS .....19

    Introduction.....19

    Materials and Methods .....21

    Results.....26

    Discussion.....27

CHAPTER 4: ASSESSMENT OF HERBIVORY ON PRE-REPRODUCTIVE *YUCCA BREVIFOLIA* WITHIN NURSE PLANT ASSOCIATIONS .....32

    Introduction.....32

    Materials and Methods .....33

    Results.....34

    Discussion.....35

CHAPTER 5: DISCUSSION .....38

APPENDIX A: TABLES AND FIGURES FOR CHAPTER 1.....44

APPENDIX B: TABLES AND FIGURES FOR CHAPTER 2.....48

APPENDIX C: TABLES AND FIGURES FOR CHAPTER 3.....55

APPENDIX D: TABLES AND FIGURES FOR CHAPTER 4.....83

LITERATURE CITED .....88

CURRICULUM VITAE .....94



## LIST OF TABLES

Table 2.1: Perennial plant species recorded within vegetation plots at the North Poleline Road and Point of Rock field sites within Dry Lake Valley .....	48
Table 3.1 (a-e): AIC <sub>c</sub> results and rankings of models examining effects of year, site, treatment, and height on soil nutrients and moisture.....	55
Table 3.2 (a-e): AIC <sub>c</sub> results and rankings of models examining effects of year, site, and treatment on <i>Y. brevifolia</i> leaf nutrients, relative water content, and growth (year not included in assessment for growth) .....	58
Table 3.3 (a-e): AIC <sub>c</sub> results and rankings of models examining effects of year, site, and treatment on <i>G. spinosa</i> leaf nutrients, relative water content, and growth (year not included in assessment for growth) .....	61
Table 3.4: Results of soil nutrient analysis.....	64
Table 3.5: Results of leaf nutrient analysis .....	71
Table 4.1: AIC <sub>c</sub> results and rankings of models examining shrub species, relative height, and degree of exposure on herbivory leaf damage to <i>Y. brevifolia</i> .....	83
Table 4.2: AIC <sub>c</sub> results for models examining the effect of treatment on herbivory leaf damage to <i>Y. brevifolia</i> from 2014 to 2015.....	84

## LIST OF FIGURES

Figure 1.1: Dry Lake Valley in central Lincoln County, Nevada, USA with field sites indicated by the orange dots.....	44
Figure 1.2: Photos of the field sites at North Poleline Road (a) and Point of Rock Road (b) .....	46
Figure 1.3: Climograph for Caliente, Nevada, USA, the closest city to the field location in Dry Lake Valley.....	47
Figure 2.1: Percentage representation of perennial plant species at North Poleline Road (a) and Point of Rock Road (b) based on vegetation plot surveys.....	50
Figure 2.2: Percentage contributions of perennial plant species to total ground cover at North Poleline Road (a) and Point of Rock Road (b) based on vegetation plot surveys .....	52
Figure 2.3: Comparisons of distances from individual <i>Y. brevifolia</i> to a random point and to the nearest plant .....	53
Figure 2.4: Perennial plant species, by percentage, with which pre-reproductive <i>Y. brevifolia</i> were found growing in proximity .....	54
Figure 3.1: Gravimetric soil moisture by year and site .....	77
Figure 3.2: Soil NO <sub>3</sub> by year .....	78
Figure 3.3: Soil NH <sub>4</sub> by year .....	79
Figure 3.4: <i>Yucca brevifolia</i> leaf K by year and treatment.....	80
Figure 3.5: <i>Yucca brevifolia</i> leaf counts by height .....	81
Figure 3.6: <i>Grayia spinosa</i> leaf P by site .....	82
Figure 4.1: The number of <i>Y. brevifolia</i> leaves showing herbivore damage plotted by the four most recorded species of nurse shrub .....	85
Figure 4.2: The number of <i>Y. brevifolia</i> leaves showing herbivore damage plotted by degrees of exposure and nurse plant species.....	86
Figure 4.3: The number of herbivore damaged <i>Y. brevifolia</i> leaves by experimental group from 2014 to 2015 .....	87

## CHAPTER 1: INTRODUCTION

Throughout the history of ecology, abiotic factors and interactions among species have both been recognized as important factors influencing community species composition. During the early part of the twentieth century in North America, the perception of plant communities and distributions of individual species was caught up within a dichotomy involving the holistic, organismal view promoted by Frederic Clements and the individualistic view held by Henry Gleason (Gleason 1926, McIntosh 1967, Callaway 2007). Clements viewed individual plant communities as super-organisms. This view emerged from his interpretation of plant community succession, which he viewed as a predictable process. For him, each stage within a successional trajectory consisted of distinct, well-defined species assemblages. The final, or climax stage, was adapted to the local abiotic conditions (McIntosh 1986). Gleason, on the other hand, argued that species are distributed independently, with each species having its own range of abiotic tolerances. Species in a given location coexisted because of overlap in these tolerances. The role that species interactions played in these interpretations also differed. According to Clements, species within a community were held together by biotic interactions, while Gleason's individualistic perspective largely disregarded such interactions. By the 1960's, Gleason's individualistic concept had become the foundation for our understanding of plant community organization.

Researchers such as Callaway (2007) have pointed out a fundamental flaw in the individualistic concept by noting that while abiotic conditions are a factor, both competition and facilitation can also play significant roles in species distributions and densities. Lortie et al. (2004) noted the need for community ecology to move beyond the individualistic concept;

however, it still underlies experimental design and the interpretation of results in plant ecology. While the influences of competition and facilitation have been well demonstrated, studies have been largely restricted to the investigation of individual species (Lortie et al. 2004).

There is a large disparity in the literature when considering the attention received by competition versus that of facilitation (Brooker et al. 2008). Historically, competition has received the most attention; however, interest in facilitation has increased considerably over recent decades (Brooker et al. 2008). Another significant development regarding these interactions is the realization that competition and facilitation do not occur in isolation of one another (Callaway and Walker 1997). Instead, the outcome of species interactions represent the sum of competition and facilitation, both of which appear to co-occur to varying degrees, depending on environmental stress (Wright et al. 2014).

The interplay between environmental stresses and biotic interactions laid the foundation for the stress-gradient hypothesis (SGH), initially proposed by Bertness and Callaway (1994). According to the SGH, the degree of abiotic stress experienced by interacting plant species influences whether the interaction is competitive or facilitative. Under benign environmental conditions, species are able to use resources efficiently and competition with other species for access to resources will be at its greatest. As species experience increasing abiotic stress, the efficiency with which they use resources decreases as well as the relative impact of competition (Wright et al. 2014). Amelioration of the abiotic stress becomes more important to survival of those species and their interaction may become more facilitative as one species ameliorates abiotic stress for the other.

When the SGH was initially proposed, it focused only on the influence of abiotic stress on interactions. Over the last several years, it has been recognized that the SGH needed to be re-evaluated as other factors affected competition – facilitation dynamic in addition to abiotic

stress. Maestre et al. (2009) argued that the type of abiotic stress (resource-limiting vs. non-resource) and the life traits (competitiveness vs. stress tolerance) of the benefactor and beneficiary species need to be considered. When the source of abiotic stress is resource-limitation, certain life trait pairings may result in scenarios in which interactions are facilitative under intermediate stress, but competitive at low (or benign) and high stress (Maestre et al. 2009, Smit et al. 2009, Louthan et al. 2014). This pattern can be further complicated if the competitiveness and/or stress tolerance of the beneficiary species changes over its life history (Maestre et al. 2009).

Herbivory is another element of the competition – facilitation dynamic that requires consideration, but has received little attention (Smit et al. 2009, Louthan et al. 2014). Juvenile plants protected by nurse plants experience less herbivore damage than if fully exposed – a phenomenon referred to as 'associational resistance' (McAuliffe 1986, Smit et al. 2009, Barbosa et al. 2009). The relationship between herbivory and plant-plant interactions has been predicted to exhibit a positive relationship with increasing herbivore impacts resulting in the increased importance of facilitation (Verwijmeren et al. 2014). However, this relationship may reach an upper limit such that the greatest facilitation occurs under intermediate herbivore pressure with continued increase in herbivore pressure resulting in the collapse of facilitation (Smit et al. 2009). Such scenarios arise either because the benefactor species experiences increased damage, lessening the concealment of the beneficiary species, or herbivores become more focused in their foraging (Verwijmeren et al. 2014). One study conducted by Louthan et al. (2014) concluded that for one beneficiary species, concealment from herbivores was more important than amelioration of abiotic stress.

Arid and semi-arid environments provide opportunities for studying the dynamic between competition and facilitation because of extreme abiotic conditions, limited water

availability, and herbivory. In these environments, facilitation plays a large role in successful germination and early survival for many plant species. Larger, older plants function as benefactors, or nurse plants, to younger individuals by ameliorating abiotic stresses (Wright et al. 2014, Verwijmeren et al. 2014), providing increased access to resources (Callaway 2007), and providing protection from herbivores (McAuliffe 1986, Flores and Jurado 2003, Drezner 2006). Initially, this association is often commensal when seedlings have no measurable impact on their nurse plant facilitators (Flores-Martinez et al. 1994, Barbour et al. 1998, Flores and Jurado 2003). However, as the seedling grows and matures, its resource requirements increase, and it becomes more competitive with its benefactor (Callaway and Walker 1997, Wright et al. 2014). Some nurse plant associations have been documented as fatal to the nurse plant as it is eventually outcompeted by the seedling it once facilitated (Callaway and Walker 1997). For example, McAuliffe (1984) concluded that an increase in dieback and mortality of *Parkinsonia microphyllum* (syn. *Cercidium microphyllum*; foothill paloverde), when in nurse plant associations with *Carnegiea gigantea* (saguaro cactus), was most likely driven by competition over soil moisture. However, it has also been suggested that such patterns could be explained as the result of the natural senescence and death of the nurse plant (McAuliffe 1984).

The recruitment of *Yucca brevifolia* (Joshua tree), an iconic plant species of the Mojave Desert, in the southwestern USA, may be dependent upon the availability of suitable nurse plant facilitators. Within near-monotypic stands of *Coleogyne ramosissima* (blackbrush), Brittingham and Walker (2000) found that a high percentage of the *Y. brevifolia* seedlings were within the canopies of woody shrubs (92.8%), despite a shrub canopy area of only 20.1%. The availability of soil moisture may be the most significant factor for *Y. brevifolia* in these associations (Brittingham and Walker 2000, Reynolds et al. 2012).

## Purpose of Study

The overall focus of this study is to gain a better understanding of how growing in proximity to desert shrubs influences the ability of pre-reproductive *Y. brevifolia* to cope with abiotic stress, resource limitation, and herbivory. According to our current understanding of facilitation and competition in interactions between plant species, pre-reproductive *Y. brevifolia* should experience facilitation by growing in proximity to shrubs while under conditions of high abiotic stress. Removal of the amelioration effect of a benefactor shrub species should result in the decreased performance and survival of *Y. brevifolia*. Shrubs may also provide associational resistance for *Y. brevifolia*. When *Y. brevifolia* are concealed or barricaded by shrubs, they should experience less herbivore damage than individuals with greater exposure. Larger *Y. brevifolia* will have greater resource requirements than smaller individuals and should be more competitive with their shrub benefactors for resources. This study examined these questions on pre-reproductive *Y. brevifolia* growing under semi-arid conditions in Dry Lake Valley, Lincoln County, Nevada, USA (Figure 1.1).

With the increasing influence of climate change, many plant species, including *Y. brevifolia*, are undergoing changes in their geographic distributions as current habitats are becoming increasingly stressful while those previously intolerable are now becoming accessible (Corlett and Westcott 2013). This pattern is apparent in southwestern Dry Lake Valley. Traveling north along North Poleline Road, one will notice that the *Y. brevifolia* become visibly smaller in stature and the population less dense, suggesting that the distribution of this species is shifting northward. The concern that has been expressed is whether populations of species like *Y. brevifolia* can shift their ranges at rates that will allow them to stay ahead of a changing climate without the need for human intervention (Corlett and

Westcott 2013). The geographic range of *Y. brevifolia* has undergone considerable contraction over the past ~11,700 years in response to climatic warming; current populations are distributed over what was once the northernmost extent of its past geographic range (Cole et al. 2010). Modeling by Cole et al. (2010) concluded that if the current trend continues, range contraction will continue, resulting in the eventual loss of *Y. brevifolia* from the southernmost part of its current range. However, Barrows and Murphy-Mariscal (2012) presented a more positive, although bittersweet, outlook; the model under their most severe climatic scenario suggested that *Y. brevifolia* may continue to persist within a refugium inside Joshua Tree National Park.

In the experimental portion of the study, I used a factorial removal experiment designed to evaluate interactions between pre-reproductive *Y. brevifolia* and *Grayia spinosa* (spiny hopsage); *G. spinosa* was predicted to function as a benefactor species in these pairwise associations. One of the goals of the experiment was to test the prediction that *Y. brevifolia* is facilitated by its proximity to *G. spinosa* because of amelioration of abiotic stress and increased resource availability.

The other question the experiment addressed was the fate of the benefactor species in these associations, specifically in this case, *G. spinosa*. Some studies (Yeaton 1978, McAuliffe 1984, 1988) have suggested the possibility that the beneficiary species may eventually competitively displace its benefactor. The fate of *Y. brevifolia* benefactors has not been previously addressed. This experiment addresses the question of whether *Y. brevifolia* associations may result in the competitive exclusion of the benefactor species.

What follows is a three-part study. The first section describes and compares the plant communities found at the two field sites established for this study. Included, was a survey that assessed the shrub species that were functioning as nurse plants to pre-reproductive *Y.*



*brevifolia*.

The second part covers a field experiment that was designed to measure potential interspecific interactions between pre-reproductive *Y. brevifolia* and the drought-deciduous desert shrub *G. spinosa*. *Grayia spinosa* was assumed to function as a nurse plant to *Y. brevifolia*. Plant removal was used as a means to try to measure facilitation and/or competition that may have been occurring between these two species and how these interactions might affect the ultimate outcome of these associations.

The third part covers a survey that investigated the effect of nurse plant associations on herbivory damage on pre-reproductive *Y. brevifolia*. The survey addressed the questions of whether the amount of cover provided by nurse plants influenced the amount of herbivory damage experienced by *Y. brevifolia* and whether the amount of damage was also influenced by the species of nurse plant. *Yucca brevifolia* involved in the field experiment were also assessed to determine if the removal of *G. spinosa* resulted in increased herbivory damage.

### **Study Location**

This study was conducted in Dry Lake Valley, located in central Lincoln County, Nevada, about 32 km west of the city of Caliente, Nevada (Figure 1.1). Dry Lake Valley, along with Delamar Valley to its south, make up the interior of a north-south oriented, closed-drainage basin that is about 132 km long and a maximum of 32 km wide (Eakin 1963). This basin is enclosed by the Pahroc Mountains to the west and the Delamar Mountains to the east. The demarcation of the two valleys loosely coincides with U.S. Highway 93, which runs east-west across the basin. The field location within Dry Lake Valley is at an elevation of about 1,524 m.

There are no climate records available for Dry Lake Valley, although the general climate has been described as semi-arid. The best possible proxy available to illustrate the climate of

Dry Lake Valley may come from nearby Caliente, Nevada (elevation about 1,524 m) (Figure 1.2, NOAA, NCEI 2015). Precipitation averages about 238 mm annually. The highest amounts of precipitation occur in late winter, decreasing to the lowest values in late spring and early summer, before peaking again in mid to late summer with the occurrence of summer storm activity. Temperatures are at their lowest during the winter months and reach a maximum during mid to late summer.

During the Pliocene and Pleistocene, Lincoln County had a much wetter climate than at present (Tschanz and Pampeyan 1970). Increased precipitation resulted in the formation of large pluvial lakes within many of the valleys. From the middle Pliocene to the early Pleistocene, both Dry Lake and Delamar Valley were occupied by one of these large, pluvial lakes. By the late Pleistocene, however, in response to drying climatic conditions following the last glacial period, the lake receded. In Dry Lake Valley, this remnant would eventually be named Pleistocene Lake Bristol. Today, playa deposits are all that remain of where Lake Bristol once occupied the valley.

Dry Lake Valley lies within an estimated 115 km wide transitional desert between the Mojave Desert to the south and the Great Basin Desert to the north (Brussard et al. 1998). Plant communities found throughout this region reflect this transition, consisting of ecotonal assemblages comprised of floristic elements from both deserts. In Dry Lake Valley, *Y. brevifolia*, an iconic species strongly associated with the Mojave Desert, is found throughout the most southeastern part of the valley. Also present are shrub species such as *G. spinosa* and *Artemisia tridentata* (big sagebrush), species that, while found in the Mojave Desert at higher elevations, are much more prominent components of the Great Basin Desert flora.

CHAPTER 2:  
DESCRIPTION OF THE PLANT COMMUNITIES OF DRY LAKE VALLEY,  
LINCOLN COUNTY, NEVADA, USA

**Introduction**

Numerous methods and metrics have been developed to assist researchers in describing and comparing the communities. A range of plant community descriptors have been used: life-form, frequency, cover, density, and biomass (Bonham 2013). For any of these descriptors, plant communities can be described by the dominance of one to a few species within a community relative to other species.

The relationship between plant interactions and plant spacing has been investigated in a number of studies (see Yeaton and Cody 1976, Phillips and MacMahon 1981, Cody 1986), especially in deserts because of their low diversity and sparse ground cover (Mahall and Callaway 1992). Phillips and MacMahon (1981) noted a relationship between shrub size and distribution pattern, with small shrubs being clumped, medium shrubs being randomly distributed, and large shrubs exhibiting a regular distribution. They attributed these patterns to the degrees of competition among individuals. Callaway and Walker (1997) also noted that spacing could be associated with ontogeny: beneficiary species, as juveniles, have closer spatial associations with their benefactors than they do as adults. This pattern reflects the greater importance of facilitation for beneficiaries at early life stages and the increasing influence of competition as the beneficiaries grow to adults.

I am interested in understanding the patterns of dominance that exist in the communities in southern Dry Lake Valley. The most conspicuous, visually dominant species in the area of study is *Y. brevifolia*. However, does this dominance extend to the other

community descriptors? Would an assessment of the species assemblages describe communities aligned with those that characterize the Mojave Desert to the south, the Great Basin Desert to the north, or a transitional desert with a mixture of floral elements from both deserts (Beatley 1976, O'Farrell and Emery 1976)?

In this study, I used survey plots that were randomly distributed across both the North Poleline Road and Point of Rock Road study sites. The vegetation within these plots was assessed to identify the common perennial plant species that characterize the field sites and describe the communities in terms of numerical dominance and contribution to ground cover. The species composition of the two communities was also compared to determine if the field sites represent two distinguishable communities or two samples of a larger community.

If successful establishment of *Y. brevifolia* is dependent upon growing in proximity to another, larger individual shrub or nurse plant, then I predicted that pre-reproductive *Y. brevifolia* would be found growing closer to other perennial plants than they would to randomly placed points. If a positive association does not exist, then I would expect there to be no noticeable difference between the distances. If larger *Y. brevifolia* eventually exclude their benefactor plant species, then I would expect there to be no difference between the distances for larger *Y. brevifolia*.

I also gathered information regarding which species function as nurse plants to *Y. brevifolia*. I investigated the frequency at which each identified shrub species was a nurse plant to *Y. brevifolia*. I compared the data recorded from the community survey plots to see if a possible correlation exists between the frequency at which a given shrub species occurs as a nurse plant and the frequency at which that species occurs at the field location and its contribution to total ground cover.

## Materials and Methods

### Species Composition and Ground Cover Survey

Two sets of 15 random points (one per study site) were mapped to each of the two study sites using QGIS (QGIS Development Team 2015). Each random point served as the center for a circular plot 2 m in radius. Within each plot, all individual woody shrubs, cacti, and *Y. brevifolia* with canopy centers within the plot were counted and identified to species level. For all individuals, canopy areas were calculated using the formula for the area of an ellipse:

$$Area = \pi \times \frac{a}{2} \times \frac{b}{2}$$

where  $a$  is the longest horizontal axis and  $b$  is the longest horizontal axis perpendicular to  $a$ .

All measurements were recorded to the nearest centimeter.

The contribution of all individuals to overall ground cover was assessed. An individual, whose entire canopy was not growing within or under the canopies of other plants, was considered as contributing to overall ground cover. Individuals whose canopies were completely within or under the canopies of other plants were considered as not contributing to overall ground cover. For individuals with canopies only partially within or under the canopies of other plants, the partial area of the canopy contributing to overall ground cover was measured using the ellipse-area formula.

The plant communities of the two sites were compared using the Sørensen-Dice presence/absence index (Gurevitch et al. 2006), which is calculated using species representation:

$$Index\ value = \frac{2a}{2a + b + c}$$

where  $a$  is the number of species found at both sites,  $b$  is the number of species found only at

the first site, and  $c$  is the number of species found only at the second site.

### Spacing of *Y. brevifolia*

Spacing of *Y. brevifolia* relative to other perennial plant species was measured to determine if *Y. brevifolia* distributions were random or non-random. Two sets of 15 random points (one set per study site) were mapped using QGIS. Measurements were recorded of the distances from each random point to the nearest individual *Y. brevifolia*, regardless of height and from the individual *Y. brevifolia* to the nearest perennial plant. *Yucca brevifolia* were grouped into size classes based on overall height: less than 1 m and greater than 1 m.

### Nurse Plant Species Survey

Another survey was conducted to determine which shrub species were potentially acting as nurse plants to *Y. brevifolia*. Two sets of 50 random points (one set per study site) were mapped using QGIS. From each random point, the distance was measured to the nearest *Y. brevifolia* that was less than 1 m in height and had no more than two rosettes. Individuals were noted as growing in the open or in proximity to a woody shrub; proximity was defined as the *Y. brevifolia* growing underneath or with some degree of physical contact with the canopy of the shrub (these same criteria are utilized in determining nurse pairs for the field experiment; see Chapter 3). If a woody shrub was involved, then the species of the shrub was identified to species level.

For all plants, canopy dimensions were measured, consisting of the longest horizontal axis followed by the longest perpendicular axis to the previous measure, and maximum height. All length measurements were recorded to the nearest centimeter.

## Results

### Species Composition and Ground Cover Survey

Twelve species were identified within the study plots at both North Poleline Road and Point of Rock Road (Table 2.1). At North Poleline Road (Figure 2.1a), *G. sarothrae* (41%) was the species with the highest density, followed by *G. spinosa* (14%), dead shrubs (15%), and *Ephedra nevadensis* (mormon tea) (10%). *Gutierrezia sarothrae* (snakeweed) (44%) also had the highest density at Point of Rock Road (Figure 2.1b). *Ephedra nevadensis* (20%) and *G. spinosa* (14%) had the second and third highest densities, respectively. *Yucca brevifolia* only accounted for 2% of the individuals occurring within the plots at North Poleline Road and 3% at Point of Rock Road. A Sørensen-Dice index value of 0.92 suggested that the two sites had similar species assemblages.

Total ground cover across both field sites was 32%. At North Poleline Road, total ground cover was 32% and dominated by *G. spinosa* (26%), *G. sarothrae* (22%), and *E. nevadensis* (21%) (Figure 2.2a). Point of Rock Road had a total ground cover of 33%, which was largely dominated by *E. nevadensis* (48%), followed by *G. sarothrae* (21%) and *G. spinosa* (20%) (Figure 2.2b). *Yucca brevifolia* individuals recorded within the vegetation plots at Point of Rock Road were all found growing under or within shrubs and therefore were not contributing to total ground cover, although there were larger, reproductive individuals that would have contributed to total ground cover had they been recorded within the plots.

#### Spacing of *Y. brevifolia*

Of the 30 individuals assessed to determine *Y. brevifolia* spacing, 14 were less than 1 m in overall height and 16 were above 1 m in overall height. For both size classes, distances between *Y. brevifolia* and perennial plants were noticeably less than the distances between *Y. brevifolia* and random points (Figure 2.3), showing that *Y. brevifolia* are growing in a non-random distribution across the two sites.

#### Nurse Plant Species Survey

*Ephedra nevadensis* (45%) was the most commonly recorded nurse shrub, followed by *G. spinosa* (25%) (Figure 2.4). Other shrub species that represented greater than 3% of the individuals recorded included *G. sarothrae* (10%), *L. andersonii* (10%), and *A. tridentata* (4%). About 4% of pre-reproductive *Y. brevifolia* were found associated with dead shrubs and none were found growing in isolation.

## Discussion

### Dominance and Community Description

The plant communities at North Poleline Road and Point of Rock Road could be described as *Y. brevifolia* woodlands, implying that *Y. brevifolia* is the dominant species in these communities. Upon a first time approach to these locations, such a conclusion would be understandable, as *Y. brevifolia* is the most noticeable species at these locations, surrounded by various shrubs and open ground. This vegetation description illustrates the importance of defining what 'dominance' means when using the term in describing plant communities.

*Yucca brevifolia* could be referred to as the visually dominant species at the study location. However, in terms of density, *G. sarothrae* dominates. Although *G. sarothrae* is the shrub with the highest density at both locations, at neither location is it the main contributor to overall ground cover. The high density of *G. sarothrae* is most likely due to its ability to rapidly colonize areas disturbed by livestock grazing (Markle 1917, Thacker et al. 2008, Ralphs and McDaniel 2011), which occurs annually at the field location roughly from late winter to the middle of spring. Considering the short life-span of *G. sarothrae*, roughly 4 to 7 years (Ralphs and McDaniel 2011), the removal of livestock grazing from the location would probably result in a rapid decline in the density of *G. sarothrae*.

Beatley (1976) described the vegetation of the Nevada Test Site in Nye County, Nevada,



about 150 km southwest of the field location in Dry Lake Valley. She described three assemblages that are found in the closed drainage basins of the transition desert: *Grayia* – *Lycium andersonii*, *Lycium pallidum* – *Grayia*, and communities dominated by *Lycium shockleyi*. Of these three, *Grayia* – *Lycium andersonii* was described as the plant association that most characterized plant communities found within these basins (Beatley 1976). The community of the field location in southern Dry Lake Valley shows a resemblance to this assemblage. *Grayia spinosa* and *L. andersonii* are both well represented, although *L. andersonii* is not considered a dominant at either of the sites. A departure from the description given by Beatley is that at my Dry Lake Valley sites, *E. nevadensis* is a dominant component. Many of the other species mentioned in Beatley's (1976) description are also present: *Atriplex canescens*, *Cylindropuntia echinocarpa*, *E. nevadensis*, *Krascheninnikovia lanata*, *Tetradymia axillaris*, *Tetradymia glabrata*, and *Y. brevifolia*. Total shrub cover in these communities was described by Beatley (1976) as ranging from 32 to 37%. The overall ground cover percentage calculated for both field sites (32%) falls at the low end of this range.

During the late 1990s, the classification of the Nevada Test Site vegetation was revisited by Ostler et al. (1999) and Hansen et al. (1999). Among their descriptions of assemblages found within the transition desert is the *E. nevadensis* – *G. spinosa* shrubland. This assemblage not only includes the named shrub species as dominants, but also *Atriplex canescens* and *Hymenoclea salsola* as co-dominants, and *L. andersonii*, *Chrysothamnus viscidiflorus*, and *Coleogyne ramosissima*, among other species present. In comparison to the field location, *L. andersonii* might be considered as a minor component, although it forms a much larger component than *A. canescens*, which is rarely encountered at the Point of Rock site. A species of *Chrysothamnus* is found nearby along U.S. Highway 93, but does not occupy either of the field sites. Neither *H. salsola* nor *C. ramosissima* are present at the field location. Based on the

data collected during the vegetation survey, I would describe the field location community as a *E. nevadensis*/*G. spinosa*/*G. sarothrae* shrubland with *Atriplex canescens*, *Cylindropuntia echinocarpa*, *Krascheninnikovia lanata*, *L. andersonii*, *Tetradymia axillaris*, *Tetradymia glabrata*, and *Y. brevifolia* as minor components.

#### Spacing of *Y. brevifolia*

The distances measured between *Y. brevifolia* less than 1 m in height and neighboring plants is consistent with previous work that emphasizes the necessity for *Y. brevifolia* to grow in proximity to other plants for establishment and survival, at least during the early part of its life history. The proximity of larger *Y. brevifolia* (greater than 1 m in height) to neighboring perennial plants may suggest that later in life, *Y. brevifolia* may themselves facilitate the establishment and growth of desert plants.

#### *Gutierrezia sarothrae* as a Nurse Plant

*Gutierrezia sarothrae* is a puzzling case. Although it constituted 10% of the shrubs pre-reproductive *Y. brevifolia* were growing in proximity to, it is not known if those *G. sarothrae* individuals were actually functioning as nurse plants or if their association represents an alternative scenario in which they, themselves, became established next to an already present pre-reproductive *Y. brevifolia*. The latter scenario may be the most likely as *G. sarothrae* is a short-lived species, with a life-span of roughly 4 to 7 years (Ralphs and McDaniel 2011). The height range of pre-reproductive *Y. brevifolia* found in proximity to *G. sarothrae* was 17 to 65 cm. Using an estimated growth rate of 3 cm/year for *Y. brevifolia* (see Comanor and Clark 2000, Gilliland et al. 2006, Esque et al. 2015), an individual 17 cm in height would be 5-6 years old, within the estimated lifespan of *G. sarothrae*, making it difficult to determine which of the two plants established first. On the other hand, a *Y. brevifolia* 65 cm in height could be 21-22 years old and unlikely to have become established under the *G. sarothrae* it was associated

with. The *Y. brevifolia* may have become established in proximity to a different shrub species, which eventually died and was replaced by *G. sarothrae*.

A third possible scenario is that a longer-lived *Y. brevifolia*, such as the example just mentioned, did become established in proximity to a *G. sarothrae*. Eventually, other individuals of *G. sarothrae* may become established in proximity to the already present *Y. brevifolia* – *G. sarothrae* pair and may serve as replacement nurse plants following the death of the initial *G. sarothrae*. This scenario would serve to allow *G. sarothrae*, as a species, to self-perpetuate itself as a nurse plant to other desert plants over extended periods.

Although an individual of *G. sarothrae* may not have played any role in facilitating *Y. brevifolia* establishment, it may still facilitate by providing some degree of protection for pre-reproductive *Y. brevifolia* that remain vulnerable to herbivory.

#### Correlation Between Total Ground Cover and Nurse Plant Frequency

A correlation can be made between the contribution to total ground cover by individual shrub species and the frequency of pre-reproductive *Y. brevifolia* plants that occur under the canopies of those species. *Ephedra nevadensis* and *G. spinosa* contributed the most to total ground cover and had the highest frequency of occurrence with pre-reproductive *Y. brevifolia*. Brittingham and Walker (2000) noted in their study that the shrub species that had the highest frequency occurrence with *Y. brevifolia* seedlings was *C. ramosissima*, which also was the largest contributor to total ground cover. However, they also noted that there were three shrub species that had *Y. brevifolia* seedlings under their canopies at higher frequencies than expected based on their contributions to total ground cover: *Ambrosia dumosa* (white bursage), *G. spinosa*, and *Krameria parvifolia* (range ratany). *Ephedra nevadensis* was among the species that had a lower occurrence of *Y. brevifolia* seedlings under its canopy than expected. This raises the question of whether there may be nurse species preference by *Y.*

*brevifolia*; seedlings may perform better when associated with certain shrub species compared to others. The possibility of species preference in positive interaction has been discussed by Callaway (1998). In this study, the most common nurse plant species of *Y. brevifolia* were also among those species that contributed the most to total ground cover. There does not appear to be evidence to suggest that any nurse species preference may exist. The comparison between total ground cover and nurse plant species uses data that were collected during two independently conducted surveys and the apparent relationship between these two data sets may only be coincidental.

CHAPTER 3:  
COMPETITIVE AND FACILITATIVE INTERACTIONS BETWEEN *YUCCA BREVIFOLIA*  
AND *GRAYIA SPINOSA* IN NURSE PLANT PAIRS

**Introduction**

Along with abiotic conditions, species interactions play a significant role in structuring plant communities. In environments that exhibit extreme abiotic stress, performance of juvenile plants is enhanced through positive interactions with the adults of other species, a phenomenon first described as the “nurse plant syndrome” by Niering et al. (1963) (see also Callaway and Walker 1997). By growing in proximity with larger adult plants, juveniles are sheltered from excessive solar radiation and extreme temperatures, and have access to increased soil moisture and nutrients (Padilla and Pugnaire 2006).

These associations, which are initially facilitative for the juvenile plant, can become increasingly competitive with the benefactor species as resource requirements of the juvenile increase as a function of size. The increase in competition may eventually result in the exclusion of the benefactor. This pattern of replacement was noted by Turner et al. (1966) when they observed *Carnegiea gigantea* (saguaro cactus) growing in proximity to dead *Parkinsonia microphyllum* (syn. *Cercidium microphyllum*; foothill paloverde). However, they attributed the demise of the paloverde to natural senescence. About fifteen years later, Vandermeer (1980) hypothesized that nurse plants of *C. gigantea* were succumbing to competitive pressure from the very individuals of *C. gigantea* they were initially facilitating. Since then, studies have investigated this shifting dynamic from facilitation to competition and the resulting outcomes of nurse plant associations. The results have been mixed: some studies have concluded eventual replacement of the benefactor by the beneficiary (see McAuliffe 1984,

1988). Other studies, while detecting increasing competition, concluded that replacement was not a pre-determined outcome (Flores-Martinez et al. 1994, Flores-Torres and Montaña 2015).

A factorial, removal field experiment was conducted from 2013 to 2014 to investigate competitive and facilitative interactions within nurse plant pairs in which pre-reproductive *Y. brevifolia* were growing in proximity to larger, mature *G. spinosa*. This experiment was conducted under conditions of high abiotic stress (temperature) and resource limitation (water) and it was expected that these conditions would best elicit responses that would indicate the kind of interactions occurring between the two plant species when one of them was removed.

The relative size of *Y. brevifolia* was considered as an influencing factor in these pairings as it was anticipated that those *Y. brevifolia* that were larger relative to their nurse counterparts would interact more competitively than smaller individuals.

In pairings involving *Y. brevifolia* that were small relative to their benefactor *G. spinosa*, it was predicted that *Y. brevifolia* were being facilitated by *G. spinosa* through abiotic stress amelioration and increased resources. At the same time, the *G. spinosa* was experiencing no noticeable competitive effects from the *Y. brevifolia*. In these pairings, I expected that the removal of *G. spinosa* would negatively impact *Y. brevifolia* as a consequence of losing the facilitative effects offered by *G. spinosa*. *Yucca brevifolia* would experience reduced soil moisture and a reduction in leaf nutrients and water status resulting from the reduced soil moisture. On the other hand, removal of *Y. brevifolia* would have no noticeable effect on *G. spinosa*. There should be little to no change in soil moisture under *G. spinosa* and in the nutrient content and water status of its leaves.

Increased growth of *Y. brevifolia* was expected to result in increased stress tolerance and resource requirements. Therefore, the interaction between larger *Y. brevifolia* and their *G.*

*spinosa* benefactors would be more competitive. In pairings with *Y. brevifolia* larger than *G. spinosa*, I expected that the removal of either of the species would result in a benefit for the remaining species as competition for resources is reduced. I predicted increases in leaf nutrients and water status for both species. Soil moisture may differ though depending on which species is removed. Soils under *G. spinosa* were expected to have an increase in soil moisture following removal of *Y. brevifolia*. Soil moisture following *G. spinosa* removal may still decrease because of reduced shading of the soil surface and the lack of shading provided by *Y. brevifolia*.

## **Materials and Methods**

### Species Pair Selection

During spring 2013, species pairs were selected that consisted of a live individual of *Y. brevifolia* and a live individual of *G. spinosa*. The *Y. brevifolia* were either growing underneath or with some degree of physical contact with the canopy of *G. spinosa*, which could have included dead branches as well as live. If an individual *Y. brevifolia* was in contact with canopies of other shrub species in addition to *G. spinosa*, then at least 75% of the visible canopy contact, based on visual estimation, had to be with *G. spinosa*. Individuals of *Y. brevifolia* could not exceed 1 m in overall height and could not have more than two rosettes. To prevent selection of clonal individuals of *Y. brevifolia*, plants had to be at least 0.5 m away from the nearest individual *Y. brevifolia* (adopted from Brittingham and Walker 2000). Heights of the plants in each pair were measured and were noted as either having *Y. brevifolia* shorter or taller than its *G. spinosa* nurse plant. A total of 144 species pairs across both sites (2 sites x 72 pairs) were selected.

### Experimental Groupings

Species pairs were randomly assigned to one of three experimental groups: a *G. spinosa* removal group, a *Y. brevifolia* removal group, or a control group with both individuals left intact. Pairs with *Y. brevifolia* shorter than their *G. spinosa* nurse shrubs were assigned treatments independently of pairs in which *Y. brevifolia* were taller. Pairs were assigned so that height differences were distributed equally across all three experimental groups.

#### Leaf Tissue Sampling and Analysis

Following group assignments and just prior to plant removal in late spring/early summer 2013, leaf samples were collected from individuals that were to be left in place during the experiment. Samples were used to assess leaf water status, in the form of Relative Water Content (RWC), and leaf nutrients in the forms of nitrogen (N), phosphorus (P), and potassium (K). Leaf samples collected for nutrient analysis were oven dried at 40°C to minimize volatilization of N.

P was of particular interest for *G. spinosa* because of the documented high levels of the cation that are sequestered within its leaf tissues (Rickard 1965, 1982, Rickard and Keough 1968). It has also been documented that leaf decomposition results in soils beneath *G. spinosa* canopies becoming enriched with K relative to soils in open areas (Rickard and Keough 1968).

Leaf samples collected for measuring RWC were placed immediately into 20 ml glass scintillation vials and kept cool in the field prior to transport to the lab. *Yucca brevifolia* leaves were cut into sections to facilitate fitting into the vials. In the lab, samples were kept in refrigeration until analysis.

Leaf relative water content was measured by first measuring the biomass of the leaf tissue inside the vials. For *Y. brevifolia* leaves, vials were opened and distilled water was added to the vial until the cut end of the leaves at the bottom of the vials was covered. For *G. spinosa*, leaves were removed from the vials and placed on distilled water-saturated filter paper in petri



dishes. Leaf tissue was allowed to hydrate for 4 hours at room temperature before biomass was again determined. Samples were then oven dried at 40°C (to minimize N volatilization) until mass loss ceased and final dry mass was recorded. Relative water content was calculated using the formula (Turner and Kramer 1980, Kirkham 2014):

$$RWC = \frac{\text{fresh weight} - \text{dry weight}}{\text{hydrated weight} - \text{dry weight}} \times 100$$

Collection of leaf tissue samples was repeated at the conclusion of the experiment in late spring 2014, near the end of the *G. spinosa* growing season. Samples were processed as previously described.

#### Soil Sampling and Analysis

In addition to leaf sampling, the top 10 cm of soil was sampled from each pair just prior to plant removal. Samples were collected within the dripline of the *G. spinosa* canopy, near the *Y. brevifolia*. Surface organic matter was scraped away just prior to sampling. To avoid repeat sampling of the exact same location at the end of the experiment, the compass aspect (relative to true north) of the sampling location was recorded relative to the center of the *G. spinosa* canopy, or, in the case when *G. spinosa* was removed, the center of the *Y. brevifolia*. Samples were used to assess gravimetric soil moisture, and soil nitrate (NO<sub>3</sub>), ammonium (NH<sub>4</sub>), P, and K. Samples were dried at 40°C to minimize volatilization of soil N. Sample collection was repeated at the conclusion of the experiment in late spring 2014, near the end of the *G. spinosa* growing season. Samples were processed as previously described.

#### Plant Measurements and Removal

Immediately prior to plant removal in late spring/early summer 2013, height measurements, to the nearest centimeter, were collected from both plants in each pair. Plants selected for removal were cut down to ground level, leaving the root systems intact to

minimize disturbance to the remaining plant(s) and surrounding soil. Over the course of the experiment, plots were re-visited periodically to remove any growth resulting from re-sprouting of cut plants.

### Measuring Plant Growth

*Yucca brevifolia* growth was assessed by counting the number of leaves produced over the course of the experiment. Terminal buds of all rosettes were marked with an oil-based paint soon after the establishment of the experimental groups and subsequent plant removals. New leaves that emerged between the painted leaves and the terminal bud of the rosette were counted. To facilitate leaf counting, fluorescent-colored twine was wrapped around each rosette at the level of the marked leaves; leaves that occurred above the twine were leaves produced since the time the terminal buds were marked. Photos were taken of all rosettes, aiming down upon the terminal bud. Leaf counts were determined from the photos using ImageJ software (Rasband 1997). Final leaf counts were tallied during the fall of 2014.

Relative growth of *G. spinosa* plants was assessed on 5 to 10 branches per shrub. Each branch, at least 5 cm in total length, with well developed buds that suggested potential for branch growth during the coming growing season, was tagged, marked, and measured prior to the start of the 2014 growing season. In the fall of 2014 following the end of the growing season, branches were re-measured. Branches that had suffered herbivory damage or had lost length, likely due to measurement error, were excluded from the final analysis. Relative growth for each individual of *G. spinosa* was determined by calculating the mean of the three longest changes in branch length for each shrub and dividing that value for each shrub by the maximum value of that metric from all of the shrubs combined:

$$\text{Relative growth} = \frac{\bar{x} \text{ of the 3 longest } \Delta \text{ branch length per shrub}}{\text{Max } \Delta \text{ branch length for all shrubs}}$$

## Data Analysis

All water status, nutrient, and growth data were analyzed using generalized linear models and model selection using the corrected Akaike information criterion (AIC<sub>c</sub>). Models assessed the main effects of treatment, height (short or tall), year, site, and combinations of these effects. A 'null' model was also included that represented the scenario in which none of the main effects influenced the data.

### Model Selection, Information Theory, and P-values

The use of model selection to evaluate scientific questions has its foundation in the Method of Multiple Working Hypotheses, which was laid out in Thomas Chamberlin's 1890 essay (which has since been reprinted in 1965 and 1995) (Chamberlin 1965, Elliott and Brook 2007). According to Chamberlin, there may be multiple valid explanations for any observed phenomenon. Single hypothesis methods, which were dominant at the time Chamberlin wrote his essay, were claimed by Chamberlin to lead researchers to favor a single hypothesis (which may or may not be supported) at the expense of other plausible explanatory hypotheses (Elliott and Brook 2007).

In this study, a set of models, each representing a possible explanatory hypothesis, was evaluated for each response variable measured. For example, the 'null' model, which will be seen multiple times throughout this manuscript, is not to be confused with a null hypothesis. The null model represents a hypothesis that states that the parameters accounted for in the other models within the model set do not help explain the pattern observed in a given response variable. Another model, the 'treatment + site' model for example, represents a hypothesis that states that a combination of experimental treatment and field site helps to explain the pattern seen in the given response variable.

The parsimony of models within a model set are determined by comparing AIC<sub>c</sub> values;

the model with the lowest value is considered the most parsimonious.  $\Delta AIC_c$  values are calculated by finding the difference between the  $AIC_c$  for a given model and the most parsimonious model. When comparing  $\Delta AIC_c$  values, models with values less than 2 are considered to have nearly as much empirical support as the most parsimonious model (Burnham and Anderson 2002, Arnold 2010). However, the simple inclusion of one additional parameter to a model may result in an increase of about 2 in the  $\Delta AIC_c$  (Burnham and Anderson 2002, Arnold 2010) and an average change of 1 in the log likelihood value (Van Belle et al. 2004), without providing any additional information to the model.

Model-selection methods and null hypothesis testing represent two different paradigms of data analysis and it has been argued that they should not be mixed (e.g. using information theory to select the most parsimonious model in a model set and then attempting to calculate a p-value to assess the strength of the most parsimonious model relative to the other models) (Burnham and Anderson 2002, Anderson and Burnham 2002). The data collected over the course of this study were evaluated by model selection using information theory (using  $AIC_c$ ). Null hypothesis testing was not employed and therefore, no p-values will be presented.

## **Results**

For most of the response variables (Table 3.1a-e, Table 3.2a-e, and Table 3.3a-e) (see Table 3.4 and Table 3.5 for results of nutrient analyses), the 'null' model came out as the model with the lowest  $AIC_c$  score, suggesting it as the most parsimonious model for the given data set. For those response variables, the addition of any one of the explanatory factors resulted in little (if any) change to the log likelihood values, suggesting that in most cases they provided no new information.

This also suggests that none of the main effects evaluated provided any additional

information, explaining none of the patterns in the data. Response variables in which the 'null' model was not selected as the most parsimonious were soil NO<sub>3</sub>, NH<sub>4</sub>, and moisture, *Y. brevifolia* leaf K and leaf production, and *G. spinosa* leaf P.

The 'year' model came out as the most parsimonious for both soil NO<sub>3</sub> and soil NH<sub>4</sub>, (Table 3.1a, Table 3.1b). Soil moisture was best fit by the 'year + site' model (Table 3.1f). *Yucca brevifolia* leaf K was best fit by the 'treatment' model (Table 3.2c). The number of *Y. brevifolia* leaves produced was best fit by the 'height' model (Table 3.2e). For *G. spinosa* leaf nutrients, P was best fit by the 'site' model (Table 3.3b).

For all response variables, the models with the second lowest AIC<sub>c</sub> scores differed from the best models by the addition of one parameter. In all cases, the additional parameter resulted in very little change in the log likelihood value, indicating that the addition of the one parameter provided no additional information that would improve the fit of the model.

## Discussion

Removal of either *Y. brevifolia* or *G. spinosa* did not result in any detectable changes in soil resources, plant nutrients, or growth that would have indicated the occurrence of facilitation or competition between the two species. Changes that were detected were attributed to changes across years, variation across the landscape, or, in the case of *Y. brevifolia* growth, height of the plant.

The model selection results for soil moisture suggest that temporal and spatial variation were most important as opposed to changes that could have been induced as a result of plant removal. However, 'site' only seems to have been a factor during sampling in 2013. Sampling at Point of Rock Road had begun shortly after sampling at North Poleline Road was completed. However, sampling had to be suspended for a period of weeks during the early summer due to

excessive heat. This may have resulted in the soil samples from Point of Rock Road being noticeably drier than those collected from North Poleline Road. With this being taken into consideration, it is reasonable to suggest that if sampling during 2013 had not been interrupted, then soil moisture for both sites may have been similar as was the case in 2014, and 'year' may have been the most parsimonious model for the data.

Soil  $\text{NO}_3$  and  $\text{NH}_4$  appear to reflect the year-to-year pattern exhibited by soil moisture.  $\text{NO}_3$  decreased from 2013 to 2014, while  $\text{NH}_4$  increased during that same period. The increased soil moisture in 2014 may have resulted in increased microbial activity that converted available  $\text{NH}_4$  into  $\text{NO}_2$  (nitrite), and in turn, into  $\text{NO}_3$ .

Among the set of models for *Y. brevifolia* leaf K, the 'treatment' model (weight of 0.31) was the most parsimonious. However, the 'null' model was competitive ( $\Delta \text{AIC}_c$  of 0.48 and weight of 0.24) and could not be discounted as a viable model. There was also a minor difference between the log likelihood values of the 'null' and 'treatment' models. This minor change in value indicates that 'treatment' is an uninformative parameter. Plotting *Y. brevifolia* leaf K as a function of treatment and year (Figure 3.4) shows that a possible difference between treatments was present at the time nurse-pairs were assigned to their experimental groups. In both 2013 and 2014, *Y. brevifolia* in the control group had higher leaf K than those in the *G. spinosa* removal group.

There are two possible explanations for *Y. brevifolia* leaf K that do not involve a treatment effect. The first is that amounts of leaf K may reflect spatial variation in the amount of soil K found across the field. During random assignment of nurse pairs to their experimental groupings, the control group was potentially assigned nurse pairs that were growing in soil with higher soil K than the *G. spinosa* removal group. However, model selection for soil K does not reflect that of leaf K. Another, perhaps more likely explanation

involves the relationship between age of *Y. brevifolia* leaves and leaf K. Wallace and Romney (1972) found that concentrations of K in *Y. brevifolia* leaves decrease as the leaves age. *Yucca brevifolia* leaves sampled during this experiment were collected from the middle of the plant, at a height between the top of the plant and the lowest green leaves. This method may have resulted in inconsistencies in the age of the leaves sampled. Leaves sampled from the *G. spinosa* removal group may have been older in age, and therefore, contained less K than those collected from the control group. In many cases, on a given plant, leaves were sampled in 2014 near where sampling occurred in 2013.

Plotting the number of *Y. brevifolia* leaves produced as a function of height (Figure 3.5) shows that individuals that were taller than their nurse plant produced more leaves than individuals that were shorter than their nurse plant. The effect of height on *Y. brevifolia* leaf production may be operating in synergy with branching. At the beginning of the study, all individuals had either one or two rosettes. At the time of the final leaf count in fall 2014, a number of individuals had branched, resulting in some having three or four rosettes.

The plotting of *G. spinosa* leaf P as a function of site (Figure 3.6) shows that individuals at Point of Rock Road had higher leaf P than individuals growing at North Poleline Road. It is unknown what mechanism(s) may be responsible for this pattern.

The absence of treatment effects may be explained by considering the individual root systems of *Y. brevifolia* and *G. spinosa*, but also of the other shrubs species found at the site as they commonly occurred in the same fertile mounds as the experimental nurse pairs. However, the literature regarding the rooting systems of desert plants is limited. Despite all of the attention received by *Y. brevifolia*, there is very little information regarding its root system; a point noted by Schwinning and Hooten (2009). An interesting account regarding *Y. brevifolia* roots came from Bowns (1973), who had *Y. brevifolia* roots in a soil pit he excavated while

studying the root system of *C. ramosissima*. In his dissertation, Bowns noted that the closest individual *Y. brevifolia* to the pit was about 11 m away, although he did not mention how large the individual was. This observation would strongly suggest that *Y. brevifolia* may be capable of accessing soils found under open areas, possibly allowing it to avoid competition with neighboring shrubs that may have more restricted root systems. Also, many *Y. brevifolia* involved in this experiment were found growing on the edges of fertile mounds. Although they most likely do not have as extensive root systems as what would be found in larger individuals, they would still potentially have access to soil resources in the adjacent open areas.

Any facilitation provided to *Y. brevifolia* outside of herbivory protection may be life stage dependent. Seedlings may benefit from the increased moisture and nutrients associated with soils under the canopies of desert shrubs. For many Mojave plant species, root biomass is mostly within the top 50 cm of soil with up to 50% of coarse root biomass at the 10-20 cm depth and fine root biomass peaking at a depth of 10-20 cm (Schwinning and Hooten 2009). Little root biomass is found in the upper 10 cm because of high soil temperatures that make it difficult to support roots (Schwinning and Hooten 2009). At the 10-20 cm depth, soil temperatures are moderate enough to support root growth, yet shallow enough to still be adequately wetted by larger precipitation events (Schwinning and Hooten 2009). High temperatures near the soil surface may provide a challenge to the establishment of seedlings in open areas including those of *Y. brevifolia*. Amelioration of surface soil temperatures as a result of shading by nurse plants may help protect the roots of seedlings until root systems can extend deeper into the soil where temperatures are cooler. The most critical time for young *Y. brevifolia* may be while the root system is penetrating down through the top layer of soil. What Bowns' observation suggests, is that eventually the root system may become rather extensive, eventually enabling the plant to acquire resources in soils of open areas, possibly avoiding competition with shrubs



whose root systems are not as laterally extensive.

Another possible explanation for the apparent lack of a treatment effect in this field experiment is that the individuals of *Y. brevifolia* selected may have already been beyond the most critical stage of their growth and had already developed a level of abiotic stress tolerance that eliminated the need for continued facilitation by *G. spinosa*. Combined with different soil niches, this factor may help explain why plant removal did not result in the detection of either facilitation or competition between *Y. brevifolia* and *G. spinosa*.

CHAPTER 4:  
ASSESSMENT OF HERBIVORY ON PRE-REPRODUCTIVE *YUCCA BREVIFOLIA*  
WITHIN NURSE PLANT ASSOCIATIONS

**Introduction**

Arid and semi-arid environments provide very limited resources for plant growth, especially water. Many perennial desert species have low growth rates (Cody 2000). Herbivory in these environments, especially by vertebrates, can be severe, not only for individuals, but also populations (Hanley et al. 2007). In response, plant species have evolved structural (spinescence and sclerophylly) (Barbour et al. 1998, Hanley et al. 2007) and chemical defenses (Barbour et al. 1998) to discourage herbivory by rodents, rabbits, hares, and larger herbivores.

Juvenile plants can avoid herbivory by growing in proximity to adult plants either through concealment or by exploiting existing anti-herbivory mechanisms provided by the associate. This phenomenon is referred to as 'associational resistance' (Smit et al. 2009, Barbosa et al. 2009).

This survey investigated herbivory experienced by pre-reproductive *Y. brevifolia* and whether the species of the nurse plant and/or the amount of protection provided by the nurse plant influenced the amount of leaf damage experienced by those *Y. brevifolia*. This question was addressed using count data collected from *Y. brevifolia* identified in the nurse plant survey described in Chapter 2.

*Yucca brevifolia* involved in the field experiment (described in Chapter 3) were evaluated for herbivory damage once it was apparent that herbivores were impacting those individuals. Herbivory on *Y. brevifolia* in the control and *G. spinosa* removal groups was measured in fall 2014 and again in fall 2015.

## Materials and Methods

This survey expanded upon the nurse plant species survey explained in Chapter 2, using the same set of nurse plants that were identified in that survey. Herbivory of *Y. brevifolia* was assessed by counting all damaged leaves (dead and alive) and measuring the number of degrees *Y. brevifolia* were exposed by their benefactors to herbivores. Degrees of exposure were measured by positioning a compass directly above the center of the *Y. brevifolia* and recording the compass aspect range (relative to true north) that the *Y. brevifolia* was exposed. This measure represented the maximum lateral openness of *Y. brevifolia* determined by looking down from the top of the shrub and was vertically limited by the height of the nurse shrub canopy. Heights of the plants were also used in this analysis, which were recorded during the nurse plant species survey.

Herbivory of *Y. brevifolia* involved in the field experiment (Chapter 3) was also assessed by counting all damaged leaves (dead and alive) on individuals in the control and *G. spinosa* removal groups. Count data were collected in fall 2014 and fall 2015.

### Data Analysis

Herbivory data were analyzed using generalized linear models and model selection using the corrected Akaike information criterion (AIC<sub>c</sub>). Models assessed the main effects of shrub species, degrees of exposure experienced by the *Y. brevifolia*, the ratio of *Y. brevifolia* height to the height of the shrub (heights were recorded during the nurse plant survey), and all combinations of these effects. The ratio of *Y. brevifolia* height to nurse shrub height represented the vertical openness of *Y. brevifolia* above the canopy of the nurse shrub with values greater than 1 indicating *Y. brevifolia* that were exposed above the nurse shrub. A 'null' model was included in the model set, representing the scenario in which none of the main

effects influenced the data.

The control and *G. spinosa* removal groups from the field experiment were evaluated to assess if there was a difference in *Y. brevifolia* leaf damage between the two groups from 2014 to 2015. Generalized linear models and AIC<sub>c</sub> were employed, comparing a 'treatment' model against a 'null' model in which treatment had no effect.

## Results

At the time the nurse plant survey was conducted, five *Y. brevifolia* individuals exhibited extensive herbivore damage; the stems of the individuals were damaged, making it impossible to accurately count damaged leaves.

Table 4.1 presents the results of model evaluation using the corrected form of Akaike Information Criteria (AIC<sub>c</sub>). The 'species + exposure' model ranked as the most parsimonious model of the nine tested. The second ranked model was the 'exposure' model ( $\Delta$  AIC<sub>c</sub> of 1.00). The 'species + exposure + height' ( $\Delta$  AIC<sub>c</sub> of 2.04) and 'exposure + height' ( $\Delta$  AIC<sub>c</sub> of 3.10) models were ranked third and fourth respectively. However, taking into consideration that both the third and fourth ranked models are the first and second ranked models plus the 'height' parameter, it can be concluded that the 'height' parameter is uninformative because its inclusion into either of the two most parsimonious models results in almost no change in log likelihood value.

Plotting *Y. brevifolia* leaf damage by shrub species suggests that the species of shrub may influence the amount of herbivory damage experienced by pre-reproductive *Y. brevifolia* (Figure 4.1). According to the plot, *Y. brevifolia* associated with *G. sarothrae* experienced more leaf damage than *E. nevadensis*, *G. spinosa*, or *L. andersonii*, with no apparent difference between those three species. The degree to which individual *Y. brevifolia* are exposed, or

open, to access by herbivores also appears to influence the amount of herbivory damage, with more exposed individuals experiencing increased damage (Figure 4.2).

At the time that the *Y. brevifolia* in the experimental treatments were evaluated in 2014, five individuals died as a result of herbivory, one individual died of unknown causes, and one individual had extensive damage prior to the start of the study, making accurate leaf counting impossible. At the time of re-evaluation in 2015, the number of *Y. brevifolia* that had succumbed to herbivory increased to six and one individual had been broken, most likely by livestock. All of these individuals were excluded from the analysis.

Assessment of *Y. brevifolia* leaf damage in the control and *G. spinosa* removal experiment groups resulted in the 'treatment' model as the most parsimonious over the 'null' model (Table 4.2). A  $\Delta AIC_c$  of 12.34 for the 'null' model and an Akaike weight of 1.00 for the 'treatment' model shows strong support for the 'treatment' model.

## Discussion

Small, pre-reproductive *Y. brevifolia* growing in closest proximity to desert shrubs are least susceptible to herbivore damage. This result suggests that the shrubs are providing at least some degree of a barrier, minimizing the area of the *Y. brevifolia* that can be accessed by herbivores. The results in Figure 4.1 suggest that the species of shrub with which the *Y. brevifolia* is involved may influence the amount of leaf damage incurred; most damage was found with *Y. brevifolia* associated with *G. sarothrae*. This pattern may be related to the growth characteristics of the individual species. *Ephedra nevadensis* can produce large crowns with very dense branching. Small *Y. brevifolia* can be very easily concealed within the crowns of *E. nevadensis*, as I can vouch for from firsthand experience trying to search through the crowns of these shrubs. If the *Y. brevifolia* is discovered, the canopy can still provide

enough of a barrier to deny any herbivore access. Both *G. spinosa* and *L. andersonii* can also provide effective anti-herbivory protection, having canopies consisting of intermeshing branches with thorn-like ultimate branches. *Gutierrezia sarothrae* has no mechanical defenses and can only protect *Y. brevifolia* through concealment.

Some plant species may avoid herbivory by growing in proximity to other species that contain unpalatable secondary compounds (Callaway et al. 2000, Smit et al. 2009, Barbosa et al. 2009). However, it is unknown if secondary compounds play any role in deterring herbivory for any of the shrub species growing at the field location. Herbivory damage by *Lepus californicus* (black-tailed jackrabbit) and/or *Sylvilagus sp.* (cottontail) on *G. spinosa* was observed over the course of this study. In addition, *G. spinosa*, which is reportedly palatable and nutritious, is grazed upon by livestock as well as wildlife, including pronghorn and bighorn sheep (Tirmenstein 1999a). *Ephedra nevadensis*, while containing tannins which may function as a deterrent, is heavily grazed by both wildlife and livestock (Grayson 2011, USDA, NRCS 2015). *Gutierrezia sarothrae* is known to be toxic to livestock, although the level of toxicity may be related, in part, to phenological stage (Tirmenstein 1999b, Ralphs 2011, Ralphs and McDaniel 2011). However, *G. sarothrae* is reportedly utilized by both mule deer and pronghorn, and in the latter case, may comprise up to 28% of its diet (USDA, NRCS 2015). *Antilocapra americana* (pronghorn) were observed at the field location, however, there was no evidence to suggest that they utilize *Y. brevifolia* as a food source. *Lycium andersonii* (Anderson wolfberry) is grazed by livestock and wild burros, although it is apparently of poor quality and usually grazed when palatable species are unavailable (Tesky 1992).

The most likely agents of *Y. brevifolia* leaf damage at the field location are *L. californicus* and/or *Sylvilagus sp.* There are multiple signs to support this assertion. Both species, especially *L. californicus* have been commonly seen at the field location over the

course of this study. Damaged leaves of *Y. brevifolia* have been close to the ground and exhibited clean, angular cuts characteristic of browsing by rabbits and hares. Only short individuals of *Y. brevifolia* had experienced herbivore damage at the top of the plant, which were at heights accessible to *L. californicus* and *Sylvivagus sp.*; taller *Y. brevifolia* did not exhibit such damage. Droppings characteristic of rabbits and hares were found in proximity to *Y. brevifolia* that experienced herbivore damage.

I conclude that pre-reproductive *Y. brevifolia* are receiving herbivory protection primarily in the form of concealment or physical barriers and not through proximity to less palatable species. In addition, I speculate that certain herbivores, *L. californicus* and *Sylvivagus sp.* in particular, may be actively searching out *Y. brevifolia*, although, there is no evidence in this study to support this claim. Targeting of pre-reproductive *Y. brevifolia* by herbivores would place increased importance on the availability of benefactor species that can provide some degree of physical protection.

## CHAPTER 5: DISCUSSION

Facilitation is very important for the successful establishment and survival of juvenile *Y. brevifolia* (Brittingham and Walker 2000, Esque et al. 2015). However, little is known about the competition – facilitation dynamic as it applies to the life history of *Y. brevifolia*. The principle goal of this study was to determine if facilitation, competition, or both could be detected in nurse plant associations in which *Y. brevifolia* was the beneficiary species, and if there is evidence to suggest that these associations may eventually result in the competitive exclusion of the benefactor species.

According to our present understanding of the relationship between the environment and species interactions as presented in the stress gradient hypothesis (SGH), competition is most influential when abiotic stresses are benign. Under those conditions, species performance is at or near optimum, and resource use is at its most efficient. As abiotic stress increases in influence, species performance declines, and facilitation becomes increasingly important to species survival. While this study was not intended or designed to be a direct testing of the SGH, the field experiment was designed with the anticipation that removal of one of the plants from a pair would elicit a response in soil resources or the water/nutrient status of the remaining plant that would have indicated whether smaller *Y. brevifolia* were facilitated and/or larger *Y. brevifolia* competitive in their interactions with their *G. spinosa* benefactors. This study also tested for evidence that continued growth of *Y. brevifolia* in these interactions would result in competitive exclusion of *Y. brevifolia* benefactors. Data was not collected along a stress gradient, which would have directly tested the SGH, but from opposite ends of a stress gradient.



The inability to detect any interactions in the experimental results may reflect the interplay of plant-plant interactions and ontogeny. Smaller, stress-intolerant *Y. brevifolia* may receive facilitation in the form of abiotic stress amelioration and resource availability. As those smaller individuals grow in size and their root systems become more expansive, they likely develop increased stress tolerance, become less reliant on their benefactor species for abiotic stress amelioration and resources, and may even become competitive with their benefactors.

Considering that *Y. brevifolia* is an iconic plant species of the Mojave Desert and that it has received considerable attention in the scientific literature, it is perplexing that the literature regarding its root system is sparse. This deficiency has been noted by Schwinning and Hooten (2009) and there seem to be only anecdotal observations that provide a few clues as to the extent of its root system. Bowns (1973) encountered *Y. brevifolia* roots in a soil pit he was excavating while studying the root system of *C. ramosissima*; the closest individual was about 11 m away. Fidelibus et al. (1996) found that the *Y. brevifolia* in their study were regularly spaced with distances between individuals averaging about 7 m. These two studies suggest that *Y. brevifolia* may develop laterally extensive root systems, possibly allowing the plant access to soil resources in open areas some distance from the shoot. This topic should be addressed because knowledge of the root system of *Y. brevifolia* is needed to better understand its soil niche and how it changes as a function of ontogeny.

*Yucca brevifolia* may only experience facilitation during the earliest period of its life history, perhaps during the period when its roots are extending through the top few centimeters of soil. Under the canopy of the benefactor, not only may soil moisture be more available, but shading should also ameliorate surface soil temperatures, which, in the open, may reach levels that are lethal for roots (Schwinning and Hooten 2009). Competition with the

benefactor may increase for a period as the *Y. brevifolia* grows, requiring more resources, and its expanding root system may increasingly occupy the space being utilized by its benefactor. As the root system becomes more extensive, the *Y. brevifolia* will begin to occupy a different soil niche than its benefactor and competition could decrease in intensity or cease. Also, by this time, *Y. brevifolia* may have become stress-tolerant enough that abiotic stress amelioration by the benefactor is no longer needed to ensure survival. This would be a possible explanation for the lack of any detectable interactions in the experimental part of this study. The majority (if not all) of *Y. brevifolia* selected for this experiment may have already developed a level of stress tolerance not present in seedlings, with root systems extensive enough that there may have been little competition with the root systems of *G. spinosa*. This scenario, however, may be dependent upon the plant species coexisting with *Y. brevifolia*. Drought-deciduous shrub species such as *G. spinosa* and *L. andersonii* have shallow root systems with low root to shoot ratios and their root biomass is largely under the shrub canopy (Manning and Groeneveld 1989, Schwinning and Hooten 2009). *Ephedra nevadensis*, while having a vertically extensive root system, does not have extensive lateral roots (Schwinning and Hooten 2009). *Yucca brevifolia* may have more difficulty avoiding competition in communities dominated by *Larrea tridentata* (creosote bush), which has a vertically and laterally extensive root system with root biomass higher in the soils of open areas than under the canopy (Schwinning and Hooten 2009). In addition, *L. tridentata* produces allelopathic exudates from its roots that inhibit root growth of other species as well as conspecifics (Mahall and Callaway 1992, Schwinning and Hooten 2009).

The herbivory survey investigated the presence and degree of associational resistance experienced by pre-reproductive *Y. brevifolia* as a result of their associations with nurse plants. This survey found a pattern of decreasing leaf damage with decreasing exposure, supporting the concept of associational resistance in these associations. Among the *Y.*

*brevifolia* in the experimental groups, there was strong evidence of increased herbivore damage on those individuals that had been completely exposed following removal of their *G. spinosa* benefactors. The results of the herbivory survey suggest that even after *Y. brevifolia* may no longer need benefactor shrubs to ameliorate abiotic stresses, they continue to be facilitated by associational resistance, possibly until they develop thick periderm on their lower stems, at which point, herbivory may no longer be detrimental to continued survival (however, see Esque et al. (2003) who documented periderm consumption by small herbivores in response to extreme forage shortage).

He and Bertness (2014) offered criticism of select studies whose outcomes did not conform to the SGH as initially proposed. They noted certain elements in those studies that contributed to the apparent lack of evidence for the SGH. They followed up their critiques with a set of suggested criteria. Studies testing the SGH should be designed to: (1) account for the fundamental and realized niches of the species of interest (both beneficiary and benefactor), (2) have multiple stress levels so a stress gradient is established during the study, and (3) hold the ontogenetic stages and identities of the beneficiary and benefactor species constant over the course of the study.

Considering the first criterion proposed by He and Bertness (2014), determining the soil niches of *Y. brevifolia* (and maybe the benefactor species) as it relates to individual size may have been an important first step that would have provided a better understanding of why no treatment effect was detected in the field experiment. From that information, the transition from stress-intolerance to stress-tolerance as a function of size could have been determined. For example, DeFalco et al. (2010) noted that among different size classes of *Y. brevifolia* that were under severe drought stress, individuals that were less than 1 m in height experienced a decrease in survivorship sooner than individuals belonging to larger size classes; larger

individuals were able to tolerate drought for longer periods of time before also experiencing decreases in survivorship. For the field experiment, insight could have been gained into when the relationship between *Y. brevifolia* and its nurse plant changes from one of facilitation to competition to neutral, if those transitions exist, by using multiple size classes. However, the shortest *Y. brevifolia* was only 18 cm at the beginning of the field experiment. Shorter individuals would have provided greater resolution, but were very rare as only one or two such individuals were found during a preliminary survey conducted prior to the start of the study.

The second criterion proposed by He and Bertness (2014) stresses measuring responses along a stress gradient. Implementing that criterion would have required setting up some stress gradient(s) as part of the overall design instead of having only two categories representing extremes of a gradient (e.g. with or without a nurse plant). A stress gradient may have been achieved through using multiple levels of water and/or nutrient supplementation. Such changes should be considered for future studies of desert shrub interactions.

As for the third criterion put forth by He and Bertness (2014), concern arose, as this study progressed, that ontogeny was not properly accounted for. Ideally, seedlings would have been among the *Y. brevifolia* selected for this study. However, as noted, *Y. brevifolia* seedlings are extremely rare. While a number of *Y. brevifolia* used in this study appeared small, they may have been at least 5-6 years old (using an estimated growth rate of 3 cm/year). As was previously discussed, these individuals may have been more stress tolerant than seedlings, and their root systems may have developed enough that there might have been little competition occurring with the root system of *G. spinosa*.

Another criticism that could be levied against this study to account for the lack of treatment effect is the duration of the experiment. It could be argued that slow rates of plant growth and nutrient cycling contributed to the lack of change between the experimental

groups and more time was needed for a noticeable pattern to develop. I would argue that the results seen in soil  $\text{NO}_3$  and  $\text{NH}_4$  suggest that one growing season is enough for noticeable changes to occur, at least in some labile variables. It may also be in the best interest of studies such as this one to keep the duration as short as possible. Study duration was a factor of concern for He and Bertness (2014), pointing out that if a study goes for too long, individuals that were juveniles at the beginning of the study, may transition to adult status, affecting the final outcome.

Further research in arid and semi-arid communities is needed to understand the connection between ontogeny and niche for desert plant species and how these affect the interactions that occur between species and shape community structure. Our rapidly changing climate adds an additional layer of complexity and urgency to understand the synergy between climate, species characteristics, and the interactions between species, in shaping the structure of communities.

## APPENDIX A:

### TABLES AND FIGURES FOR CHAPTER 1

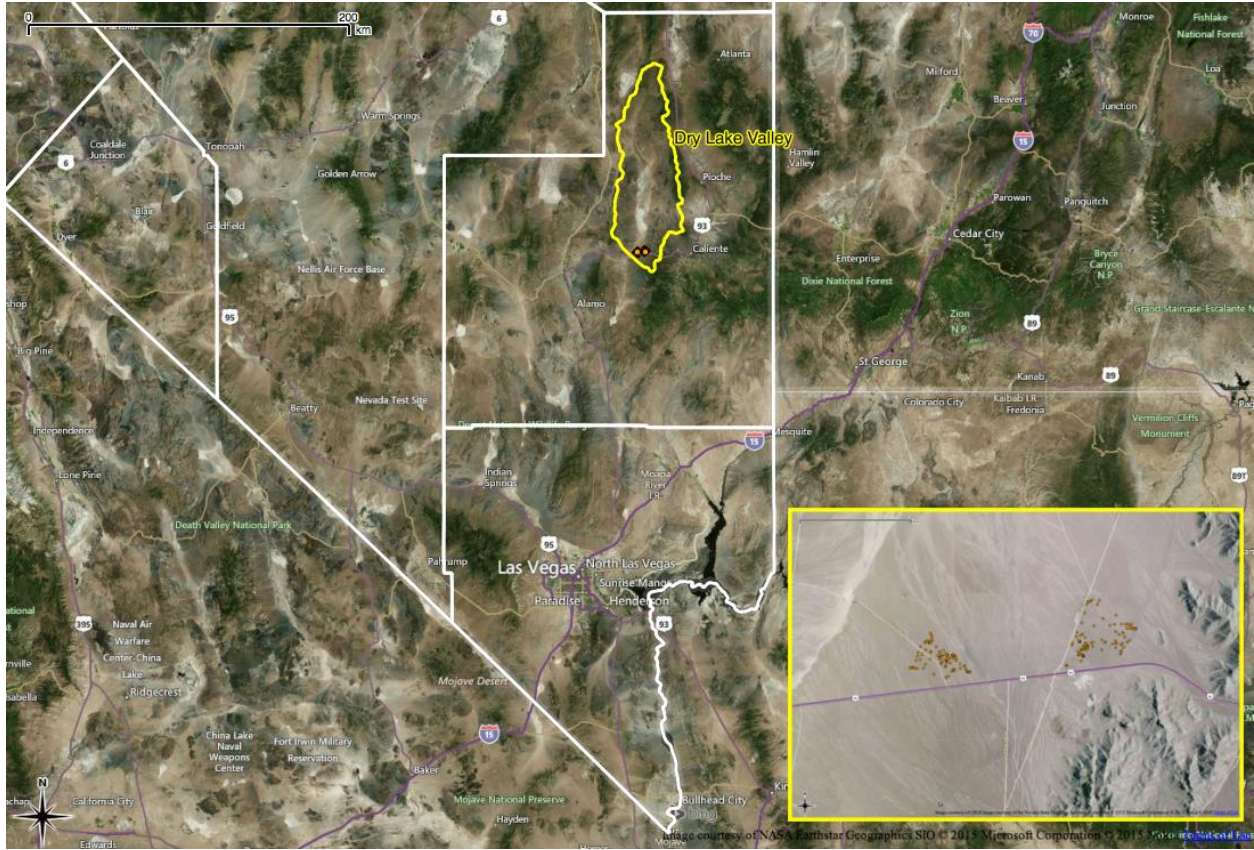


Figure 1.1: Dry Lake Valley in central Lincoln County, Nevada, USA with field sites indicated by the orange dots. The inset on the lower right shows a closer view of the two field sites. Orange dots in the inset show the location of nurse-pairs used in the field experiment. The Point of Rock Road site represented by the left side grouping, the North Poleline Road site is on the right.

a.



b.



Figure 1.2: Photos of the field sites at North Poleline Road (a) and Point of Rock Road (b).



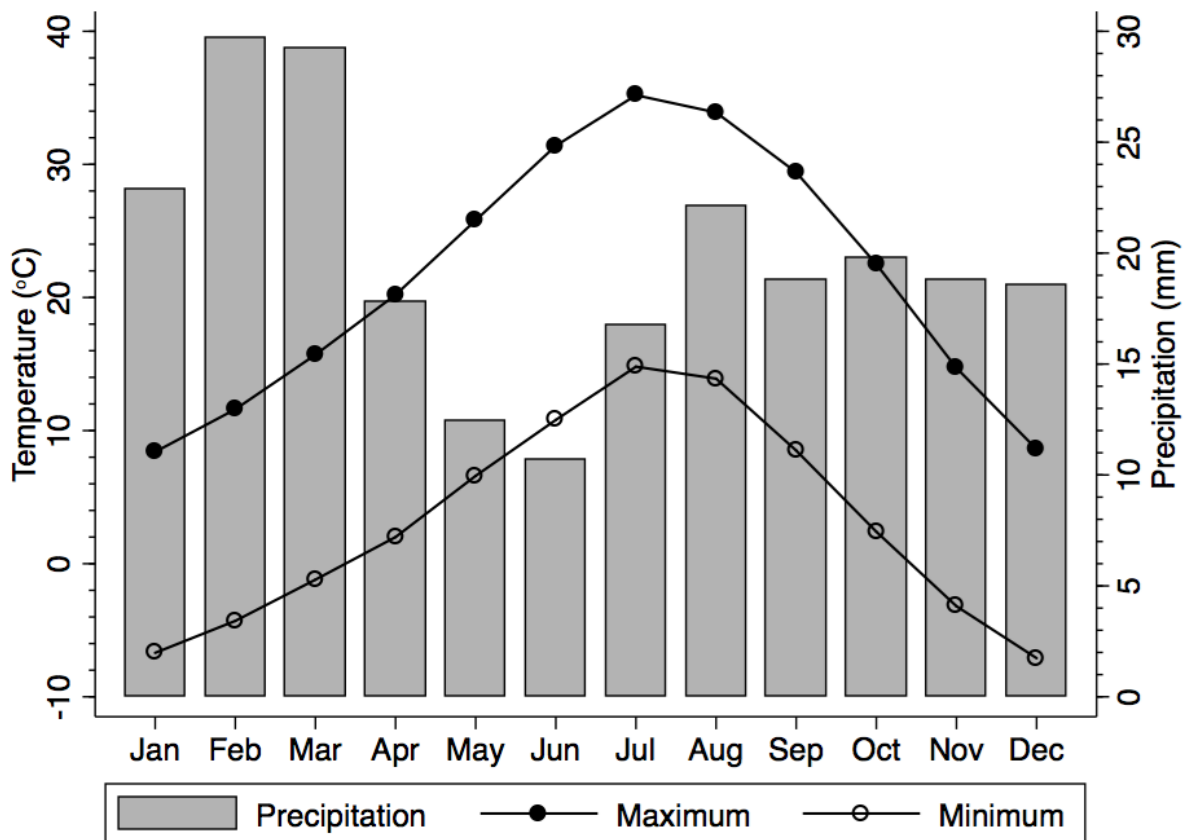


Figure 1.3: Climograph for Caliente, Nevada, USA, the closest city to the field location in Dry Lake Valley. Data was collected from the NCEI NOAA 1981-2010 climate monthly normals for Caliente, Nevada, USA (<http://www.ncei.noaa.gov>).

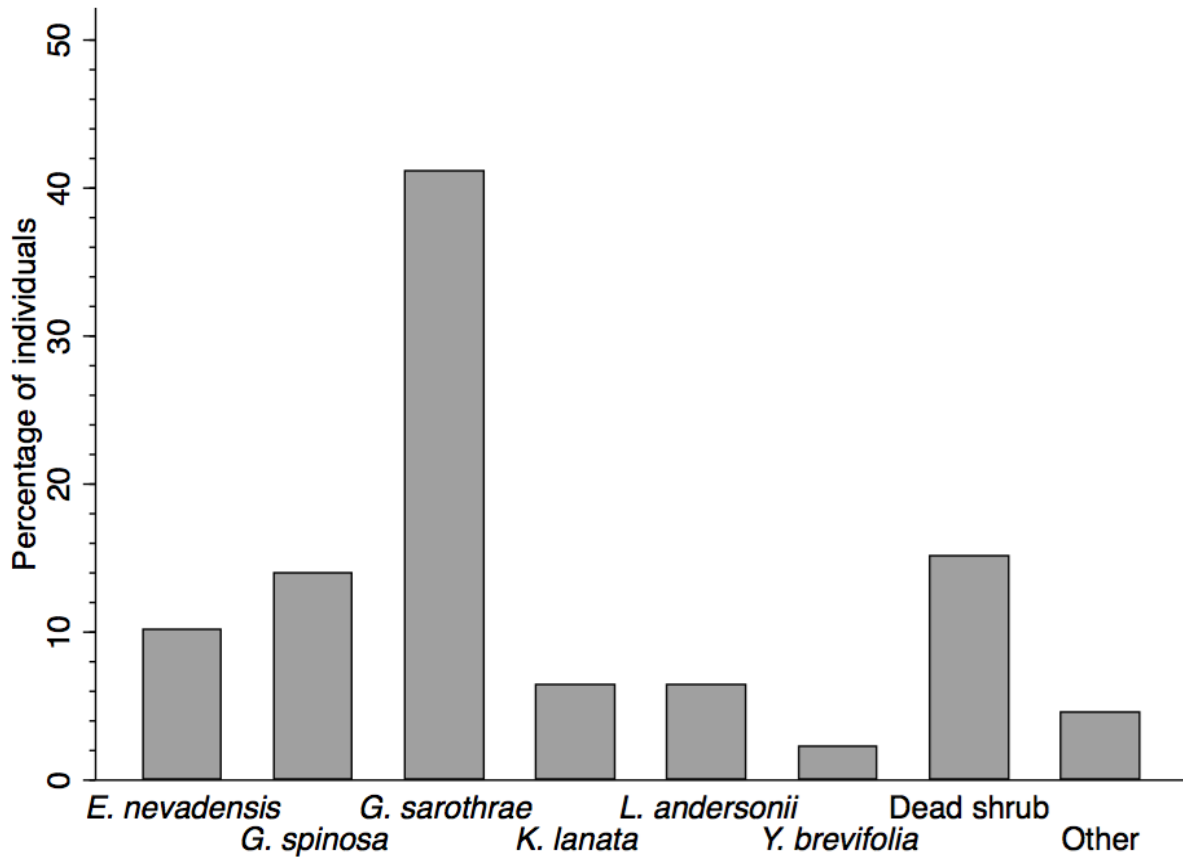
APPENDIX B:

TABLES AND FIGURES FOR CHAPTER 2

Table 2.1: Perennial plant species recorded within vegetation plots at the North Poleline Road and Point of Rock field sites within Dry Lake Valley.

North Poleline Road	Point of Rock Road
<i>Artemisia tridentata</i>	<i>Artemisia tridentata</i>
<i>Cylindropuntia echinocarpa</i>	<i>Cylindropuntia echinocarpa</i>
<i>Ephedra nevadensis</i>	<i>Ephedra nevadensis</i>
<i>Escobaria vivipara</i>	-----
<i>Grayia spinosa</i>	<i>Grayia spinosa</i>
<i>Gutierrezia sarothrae</i>	<i>Gutierrezia sarothrae</i>
<i>Krascheninnikovia lanata</i>	<i>Krascheninnikovia lanata</i>
<i>Lycium andersonii</i>	<i>Lycium andersonii</i>
<i>Opuntia erinacea</i>	<i>Opuntia erinacea</i>
<i>Tetradymia axillaris</i>	<i>Tetradymia axillaris</i>
<i>Tetradymia glabrata</i>	<i>Tetradymia glabrata</i>
<i>Yucca brevifolia</i>	<i>Yucca brevifolia</i>

a.



b.

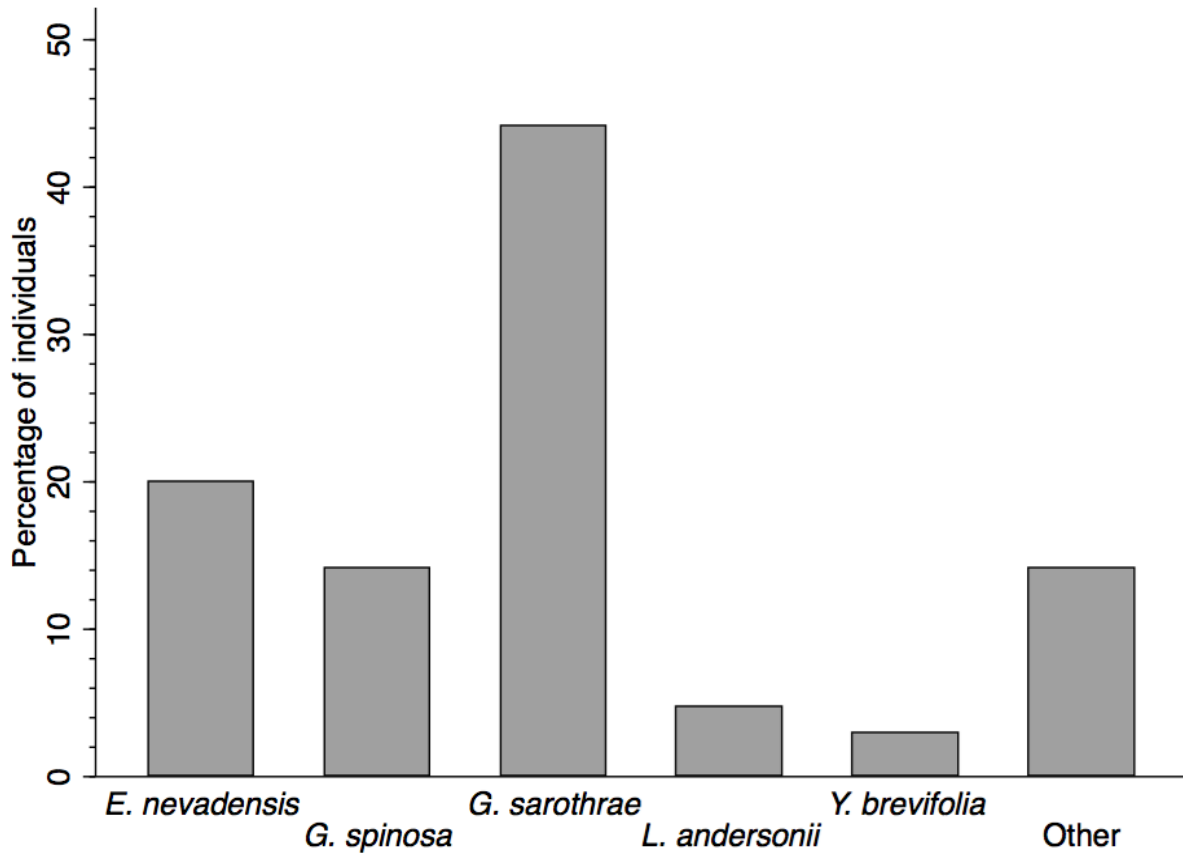
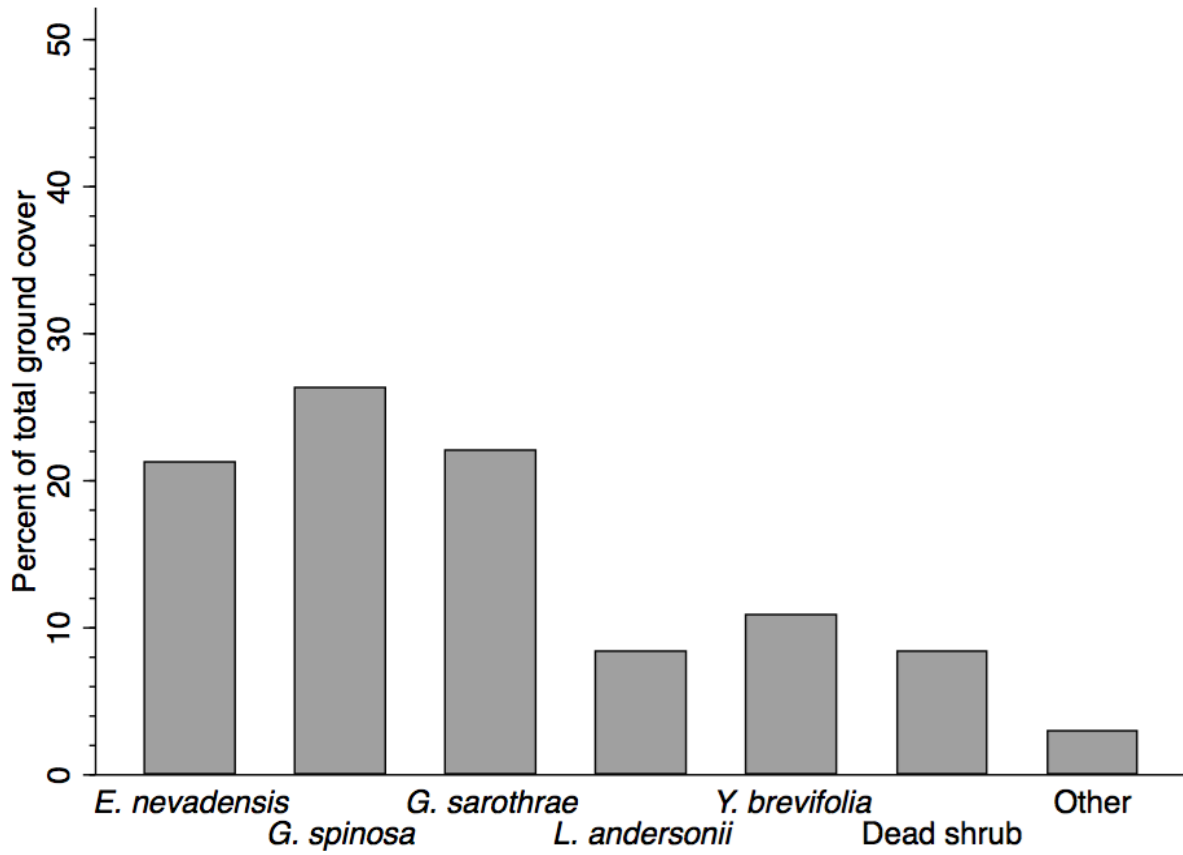


Figure 2.1: Percentage representation of perennial plant species at North Poleline Road (a) and Point of Rock Road (b) based on vegetation plot surveys. The 'other' group represents minor representative species, dead shrubs, and dead cacti that each contributed less than 3% of the individuals recorded.

a.



b.

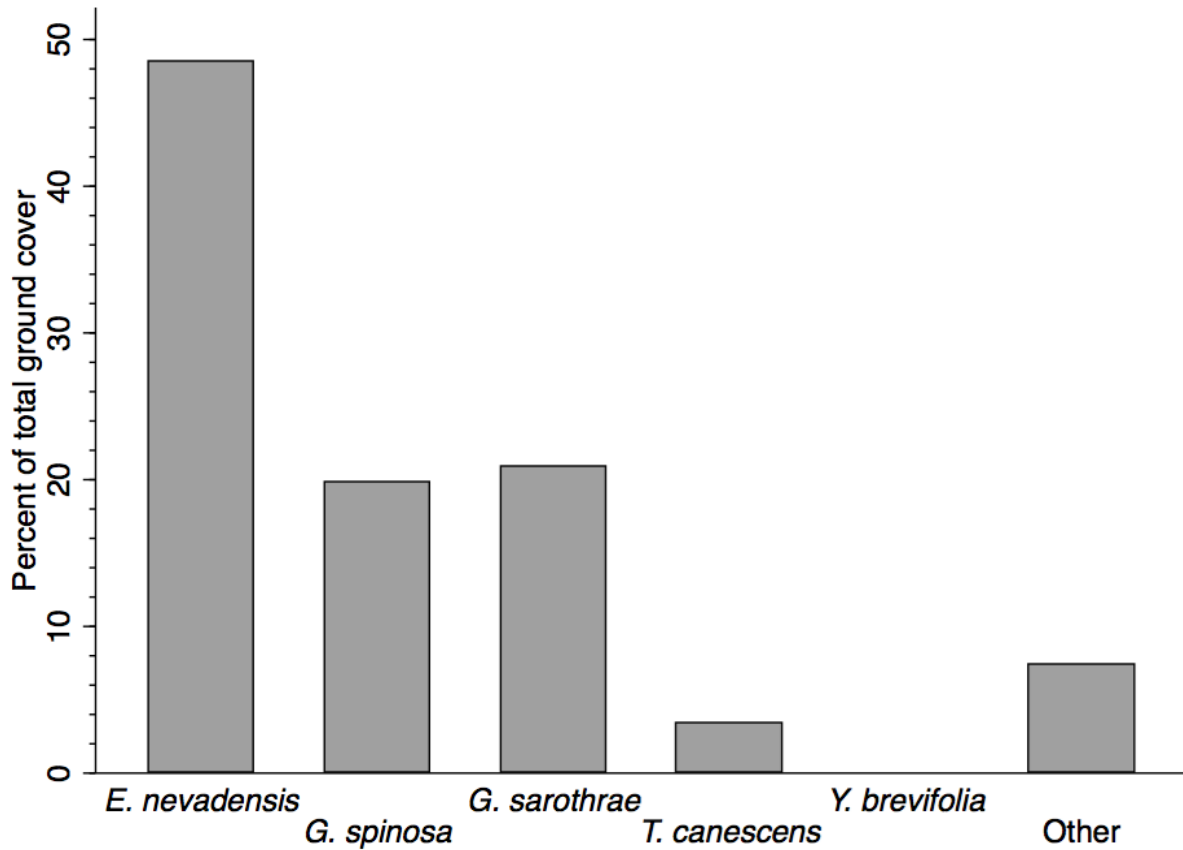


Figure 2.2: Percentage contributions of perennial plant species to total ground cover at North Poleline Road (a) and Point of Rock Road (b) based on vegetation plot surveys. The 'other' group represents minor representative species, dead shrubs, and dead cacti that each contributed less than 3% to overall ground cover with the exception of *Y. brevifolia*.

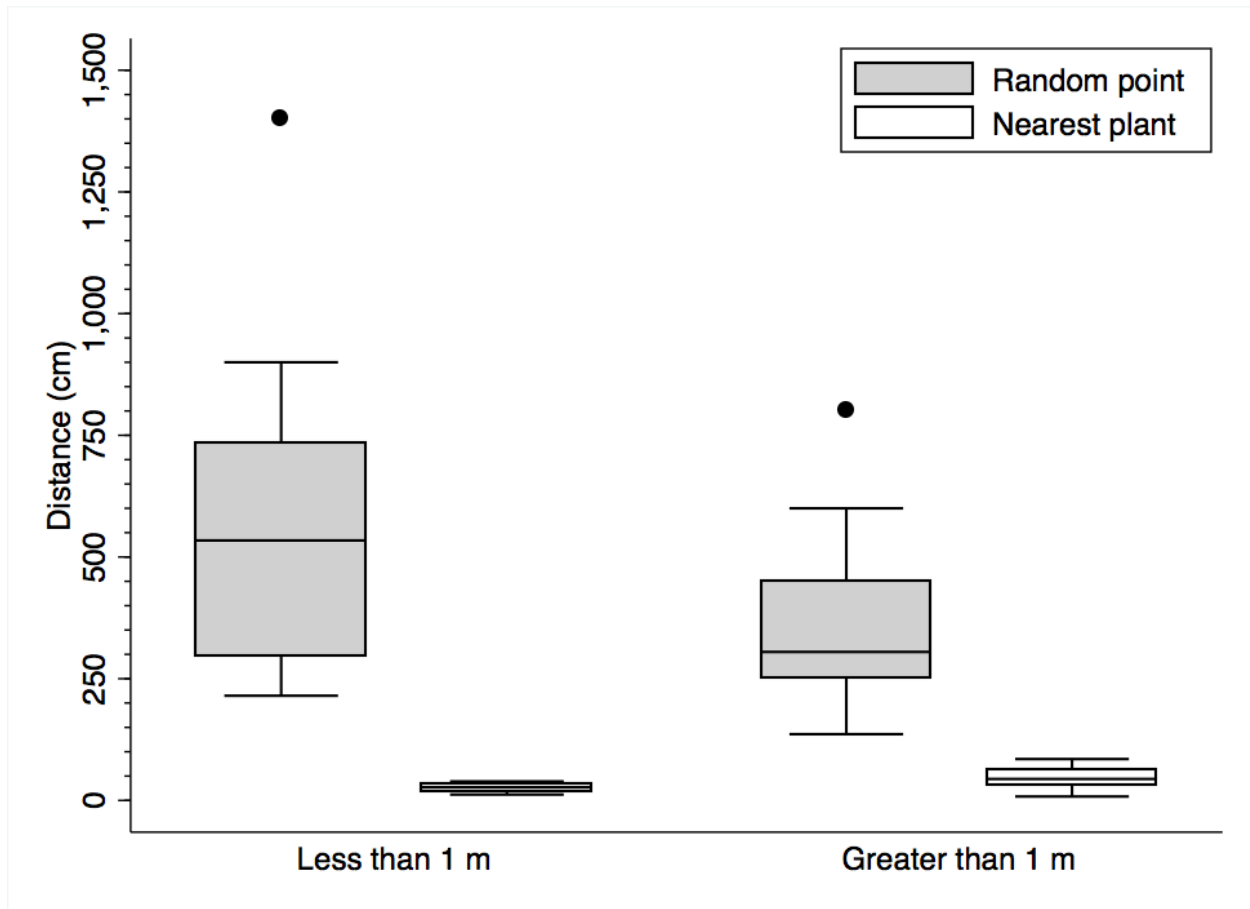


Figure 2.3: Comparisons of distances from individual *Y. brevifolia* to a random point and to the nearest plant. Data was grouped based on whether individual *Y. brevifolia* were less or greater than 1 m in overall height.

Box plots are comprised of 4 parts: the central 'box' of the plot represents the interquartile range (IQR), or central 50 percent of the data. The base of the IQR represents the 25<sup>th</sup> percentile and the top of the IQR represents the 75<sup>th</sup> percentile. The central line within the IQR represents the 50<sup>th</sup> percentile, or median of the data. The lines, or 'whiskers' protruding from the base and top of the IQR represent the bottom and top 25<sup>th</sup> quartiles of the data, respectively. The dots that may be present beyond the whiskers represent data outliers. When comparing two box plots, the medians are considered to be different if at least the median of one box plot lies outside the IQR of the other. Krzywinski and Altman (2014) provide a useful introduction to interpreting and using box plots.

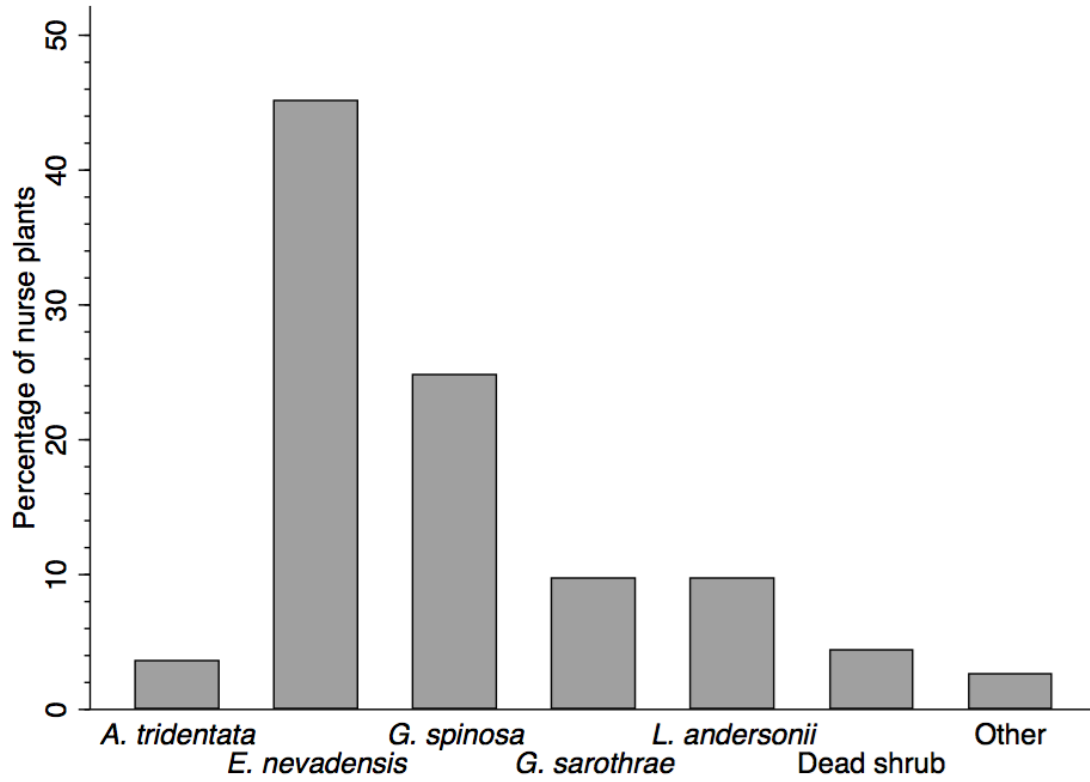


Figure 2.4: Perennial plant species, by percentage, with which pre-reproductive *Y. brevifolia* were found growing in proximity. The 'other' group includes shrub species that made up less than 3% of individuals recorded.



APPENDIX C:

TABLES AND FIGURES FOR CHAPTER 3

Table 3.1 (a-e): AIC<sub>c</sub> results and rankings of models examining effects of year, site, treatment, and height on soil nutrients and moisture.

a.

Soil NO <sub>3</sub>							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
Null	-262.89	2	527.91	5	2.64	0.07	3.75
Treatment	-261.95	3	530.16	11	4.89	0.02	11.55
<b>Year</b>	<b>-260.50</b>	<b>3</b>	<b>525.27</b>	<b>1</b>	<b>0.00</b>	<b>0.27</b>	<b>1.00</b>
Site	-262.38	3	529.02	8	3.75	0.04	6.52
Year + treatment	-260.02	4	528.47	7	3.20	0.05	4.96
Year + site	-259.72	4	525.89	2	0.62	0.20	1.36
Site + treatment	-261.52	4	531.48	12	6.21	0.01	22.35
Year + site + treatment	-259.32	5	529.30	9	4.03	0.04	7.49
Treatment + height	-259.98	4	528.40	6	3.13	0.06	4.79
Year + treatment + height	-257.95	5	526.57	3	1.30	0.14	1.92
Site + treatment + height	-259.74	5	530.14	10	4.87	0.02	11.44
Year + site + treatment + height	-257.48	6	527.90	4	2.63	0.07	3.72

b.

Soil NH <sub>4</sub>							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
Null	-218.94	2	440.01	6	6.46	0.02	25.31
Treatment	-218.69	3	443.65	9	10.10	0.00	155.64
<b>Year</b>	<b>-214.65</b>	<b>3</b>	<b>433.55</b>	<b>1</b>	<b>0.00</b>	<b>0.58</b>	<b>1.00</b>
Site	-218.65	3	441.56	8	8.01	0.01	54.90
Year + treatment	-214.30	4	437.05	3	3.50	0.10	5.75
Year + site	-214.63	4	435.69	2	2.14	0.20	2.92
Site + treatment	-218.40	4	445.24	10	11.69	0.00	345.51
Year + site + treatment	-214.29	5	439.25	4	5.70	0.03	17.26
Treatment + height	-218.69	4	445.81	11	12.26	0.00	460.28
Year + treatment + height	-214.30	5	439.27	5	5.72	0.03	17.49
Site + treatment + height	-218.40	5	447.46	12	13.91	0.00	1049.67
Year + site + treatment + height	-214.29	6	441.52	7	7.97	0.01	53.84

c.

Soil P							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
<b>Null</b>	<b>-508.36</b>	<b>2</b>	<b>1018.85</b>	<b>1</b>	<b>0.00</b>	<b>0.38</b>	<b>1.00</b>
Treatment	-507.48	3	1021.22	4	2.37	0.12	3.26
Year	-508.36	3	1020.98	3	2.13	0.13	2.90
Site	-508.24	3	1020.74	2	1.89	0.15	2.58
Year + treatment	-507.47	4	1023.39	8	4.54	0.04	9.67
Year + site	-508.24	4	1022.91	5	4.06	0.05	7.62
Site + treatment	-507.33	4	1023.11	6	4.26	0.05	8.41
Year + site + treatment	-507.33	5	1025.33	10	6.48	0.01	25.49
Treatment + height	-507.47	4	1023.38	7	4.53	0.04	9.62
Year + treatment + height	-507.47	5	1025.60	11	6.75	0.01	29.22
Site + treatment + height	-507.33	5	1025.32	9	6.47	0.02	25.39
Year + site + treatment + height	-507.32	6	1027.59	12	8.74	0.00	78.92

d.

Soil K							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
<b>Null</b>	<b>-764.70</b>	<b>2</b>	<b>1531.52</b>	<b>1</b>	<b>0.00</b>	<b>0.42</b>	<b>1.00</b>
Treatment	-764.16	3	1534.59	4	3.07	0.09	4.64
Year	-764.68	3	1533.62	3	2.10	0.15	2.86
Site	-764.60	3	1533.45	2	1.93	0.16	2.63
Year + treatment	-764.15	4	1536.74	8	5.22	0.03	13.62
Year + site	-764.58	4	1535.59	5	4.07	0.05	7.65
Site + treatment	-764.06	4	1536.57	6	5.05	0.03	12.49
Year + site + treatment	-764.05	5	1538.76	10	7.24	0.01	37.35
Treatment + height	-764.11	4	1536.66	7	5.14	0.03	13.08
Year + treatment + height	-764.10	5	1538.86	11	7.34	0.01	39.32
Site + treatment + height	-764.00	5	1538.67	9	7.15	0.01	35.76
Year + site + treatment + height	-763.99	6	1540.92	12	9.40	0.00	109.72

e.

Gravimetric soil moisture							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
Null	-124.13	2	250.31	8	235.78	0.00	1.58E+51
Treatment	-124.10	3	254.29	10	239.76	0.00	1.15E+52
Year	-43.57	3	91.22	4	76.69	0.00	4.50E+16
Site	-122.85	3	249.79	7	235.26	0.00	1.22E+51
Year + treatment	-43.55	4	95.24	5	80.71	0.00	3.35E+17
<b>Year + site</b>	<b>-4.19</b>	<b>4</b>	<b>14.53</b>	<b>1</b>	<b>0.00</b>	<b>0.75</b>	<b>1.00</b>
Site + treatment	-122.80	4	253.74	9	239.21	0.00	8.77E+51
Year + site + treatment	-3.88	5	17.97	2	3.44	0.13	5.59
Treatment + height	-123.98	4	256.10	12	241.57	0.00	2.86E+52
Year + treatment + height	-43.47	5	97.15	6	82.62	0.00	8.72E+17
Site + treatment + height	-122.59	5	255.39	11	240.86	0.00	2.00E+52
Year + site + treatment + height	-3.00	6	18.29	3	3.76	0.11	6.57

Table 3.2 (a-e): AIC<sub>c</sub> results and rankings of models examining effects of year, site, treatment, and height on *Y. brevifolia* leaf nutrients, relative water content, and growth (year not included in assessment for growth).

a.

<i>Y. brevifolia</i> leaf N							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
<b>Null</b>	<b>-72.65</b>	<b>2</b>	<b>147.49</b>	<b>1</b>	<b>0.00</b>	<b>0.38</b>	<b>1.00</b>
Treatment	-72.63	3	149.66	4	2.17	0.13	2.95
Year	-72.62	3	149.64	3	2.15	0.13	2.93
Site	-72.51	3	149.42	2	1.93	0.14	2.62
Year + treatment	-72.60	4	151.88	7	4.39	0.04	8.97
Year + site	-72.48	4	151.63	5	4.14	0.05	7.93
Site + treatment	-72.49	4	151.65	6	4.16	0.05	8.01
Year + site + treatment	-72.46	5	153.95	9	6.46	0.01	25.23
Treatment + height	-72.63	4	151.93	8	4.44	0.04	9.23
Year + treatment + height	-72.60	5	154.23	11	6.74	0.01	29.13
Site + treatment + height	-72.49	5	154.01	10	6.52	0.01	26.01
Year + site + treatment + height	-72.46	6	156.39	12	8.90	0.00	85.43

b.

<i>Y. brevifolia</i> leaf P							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
<b>Null</b>	<b>58.91</b>	<b>2</b>	<b>-115.62</b>	<b>1</b>	<b>0.00</b>	<b>0.35</b>	<b>1.00</b>
Treatment	58.91	3	-113.42	3	2.20	0.12	3.01
Year	58.91	3	-113.42	4	2.20	0.12	3.01
Site	59.33	3	-114.26	2	1.36	0.18	1.98
Year + treatment	58.91	4	-111.14	8	4.48	0.04	9.41
Year + site	59.33	4	-111.98	6	3.64	0.06	6.19
Site + treatment	59.33	4	-111.98	5	3.64	0.06	6.18
Year + site + treatment	59.33	5	-109.62	10	6.00	0.02	20.12
Treatment + height	58.91	4	-111.14	7	4.48	0.04	9.41
Year + treatment + height	58.91	5	-108.78	11	6.84	0.01	30.62
Site + treatment + height	59.34	5	-109.62	9	6.00	0.02	20.08
Year + site + treatment + height	59.34	6	-107.17	12	8.45	0.01	68.21

c.

<i>Y. brevifolia</i> leaf K							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
Null	-88.47	2	179.14	2	0.48	0.21	1.27
<b>Treatment</b>	<b>-87.13</b>	<b>3</b>	<b>178.66</b>	<b>1</b>	<b>0.00</b>	<b>0.26</b>	<b>1.00</b>
Year	-88.42	3	181.25	7	2.59	0.07	3.65
Site	-88.38	3	181.17	6	2.51	0.07	3.51
Year + treatment	-87.08	4	180.84	4	2.18	0.09	2.98
Year + site	-88.34	4	183.38	11	4.72	0.02	10.58
Site + treatment	-87.04	4	180.78	3	2.12	0.09	2.88
Year + site + treatment	-87.00	5	183.06	8	4.40	0.03	9.03
Treatment + height	-87.10	4	180.89	5	2.23	0.09	3.05
Year + treatment + height	-87.06	5	183.16	10	4.50	0.03	9.51
Site + treatment + height	-87.02	5	183.09	9	4.43	0.03	9.14
Year + site + treatment + height	-86.98	6	185.47	12	6.81	0.01	30.06

d.

<i>Y. brevifolia</i> relative water content							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
<b>Null</b>	<b>-1008.37</b>	<b>2</b>	<b>2018.81</b>	<b>1</b>	<b>0.00</b>	<b>0.36</b>	<b>1.00</b>
Treatment	-1008.37	3	2020.86	3	2.05	0.13	2.79
Year	-1008.37	3	2020.88	4	2.07	0.13	2.81
Site	-1008.35	3	2020.83	2	2.02	0.13	2.75
Year + treatment	-1008.37	4	2022.95	8	4.14	0.05	7.94
Year + site	-1008.35	4	2022.92	6	4.11	0.05	7.81
Site + treatment	-1008.34	4	2022.91	5	4.10	0.05	7.76
Year + site + treatment	-1008.34	5	2025.02	10	6.21	0.02	22.32
Treatment + height	-1008.36	4	2022.94	7	4.13	0.05	7.87
Year + treatment + height	-1008.36	5	2025.05	11	6.24	0.02	22.64
Site + treatment + height	-1008.34	5	2025.01	9	6.20	0.02	22.16
Year + site + treatment + height	-1008.34	6	2027.14	12	8.33	0.01	64.49

e.

<i>Y. brevifolia</i> leaf counts							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	$\Delta$ AIC <sub>c</sub>	Akaike weight	Evidence ratio
Null	-507.45	2	1017.05	3	2.74	0.12	3.93
Treatment	-507.45	3	1019.19	6	4.88	0.04	11.46
Site	-506.94	3	1018.17	5	3.86	0.07	6.88
Site + treatment	-506.94	4	1020.35	7	6.04	0.02	20.50
<b>Height</b>	<b>-505.02</b>	<b>3</b>	<b>1014.31</b>	<b>1</b>	<b>0.00</b>	<b>0.49</b>	<b>1.00</b>
Treatment + height	-504.99	4	1016.45	2	2.14	0.17	2.92
Site + treatment + height	-504.64	5	1018.00	4	3.69	0.08	6.34

Table 3.3 (a-e): AIC<sub>c</sub> results and rankings of models examining effects of year, site, treatment, and height on *G. spinosa* leaf nutrients, relative water content, and growth (year not included in assessment for growth).

a.

<i>G. spinosa</i> leaf N							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
<b>Null</b>	<b>-77.77</b>	<b>2</b>	<b>157.73</b>	<b>1</b>	<b>0.00</b>	<b>0.29</b>	<b>1.00</b>
Treatment	-77.76	3	159.93	4	2.20	0.10	3.00
Year	-77.37	3	159.15	3	1.42	0.14	2.03
Site	-77.16	3	158.73	2	1.00	0.18	1.65
Year + treatment	-77.37	4	161.42	7	3.69	0.05	6.33
Year + site	-76.79	4	160.25	5	2.52	0.08	3.53
Site + treatment	-77.16	4	161.00	6	3.27	0.06	5.13
Year + site + treatment	-76.78	5	162.60	9	4.87	0.03	11.42
Treatment + height	-77.75	4	162.19	8	4.46	0.03	9.29
Year + treatment + height	-77.36	5	163.76	11	6.03	0.01	20.43
Site + treatment + height	-77.15	5	163.33	10	5.60	0.02	16.45
Year + site + treatment + height	-76.77	6	165.02	12	7.29	0.01	38.27

b.

<i>G. spinosa</i> leaf P							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
Null	92.79	2	-183.38	2	1.55	0.15	2.18
Treatment	92.79	3	-181.17	6	3.76	0.05	6.55
Year	93.04	3	-181.68	5	3.25	0.07	5.07
<b>Site</b>	<b>94.67</b>	<b>3</b>	<b>-184.93</b>	<b>1</b>	<b>0.00</b>	<b>0.34</b>	<b>1.00</b>
Year + treatment	93.04	4	-179.40	9	5.53	0.02	15.84
Year + site	94.96	4	-183.24	3	1.69	0.14	2.33
Site + treatment	94.67	4	-182.66	4	2.27	0.11	3.12
Year + site + treatment	94.96	5	-180.89	7	4.04	0.04	7.55
Treatment + height	92.87	4	-179.07	10	5.86	0.02	18.74
Year + treatment + height	93.14	5	-177.24	12	7.69	0.01	46.72
Site + treatment + height	94.75	5	-180.46	8	4.47	0.04	9.35
Year + site + treatment + height	95.05	6	-178.63	11	6.30	0.01	23.36

c.

<i>G. spinosa</i> leaf K							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
<b>Null</b>	<b>-187.73</b>	<b>2</b>	<b>377.65</b>	<b>1</b>	<b>0.00</b>	<b>0.39</b>	<b>1.00</b>
Treatment	-187.72	3	379.84	4	2.19	0.13	2.99
Year	-187.69	3	379.79	3	2.14	0.13	2.91
Site	-187.68	3	379.75	2	2.10	0.13	2.86
Year + treatment	-187.68	4	382.05	7	4.40	0.04	9.01
Year + site	-187.64	4	381.96	5	4.31	0.04	8.62
Site + treatment	-187.67	4	382.02	6	4.37	0.04	8.87
Year + site + treatment	-187.63	5	384.30	9	6.65	0.01	27.81
Treatment + height	-187.72	4	382.12	8	4.47	0.04	9.33
Year + treatment + height	-187.68	5	384.40	11	6.75	0.01	29.21
Site + treatment + height	-187.67	5	384.37	10	6.72	0.01	28.78
Year + site + treatment + height	-187.63	6	386.74	12	9.09	0.00	93.93

d.

<i>G. spinosa</i> relative water content							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
<b>Null</b>	<b>-912.49</b>	<b>2</b>	<b>1827.06</b>	<b>1</b>	<b>0.00</b>	<b>0.37</b>	<b>1.00</b>
Treatment	-912.48	3	1829.11	2	2.05	0.13	2.78
Year	-912.49	3	1829.13	3	2.07	0.13	2.81
Site	-912.49	3	1829.13	4	2.07	0.13	2.81
Year + treatment	-912.48	4	1831.20	6	4.14	0.05	7.93
Year + site	-912.49	4	1831.22	8	4.16	0.05	8.02
Site + treatment	-912.48	4	1831.21	7	4.15	0.05	7.95
Year + site + treatment	-912.48	5	1833.33	11	6.27	0.02	22.94
Treatment + height	-912.48	4	1831.20	5	4.14	0.05	7.92
Year + treatment + height	-912.47	5	1833.32	9	6.26	0.02	22.87
Site + treatment + height	-912.48	5	1833.32	10	6.26	0.02	22.90
Year + site + treatment + height	-912.47	6	1835.47	12	8.41	0.01	67.01



e.

<i>G. spinosa</i> growth							
Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	$\Delta$ AIC <sub>c</sub>	Akaike weight	Evidence ratio
<b>Null</b>	<b>18.75</b>	<b>2</b>	<b>-35.35</b>	<b>1</b>	<b>0.00</b>	<b>0.38</b>	<b>1.00</b>
Treatment	18.85	3	-33.39	3	1.96	0.14	2.67
Site	19.54	3	-34.76	2	0.59	0.28	1.34
Site + treatment	19.57	4	-32.62	4	2.73	0.10	3.91
Treatment + height	19.08	4	-31.64	5	3.71	0.06	6.38
Site + treatment + height	19.93	5	-31.07	6	4.28	0.04	8.51

Table 3.4: Results of soil nutrient analysis.

Year	Site	Group	Soil nutrients												
			Dry Gravimetric Weight (%)	Total Exchange Capacity (meq/100 g)	pH	Organic Matter (%)	S (ppm)	P (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	Al (mg/kg)	NO <sub>3</sub> (ppm)	NH <sub>4</sub> (ppm)
2013	North Poleline	Control	0.184	27.08	8.8	0.90	16	63	3995	565	633	17	145	2.1	3.7
2013	North Poleline	Control	0.310	25.68	8.8	1.02	18	71	3307	680	1064	18	244	2.2	3.0
2013	North Poleline	Control	0.234	30.97	8.8	1.12	24	105	4603	624	722	22	109	2.5	5.9
2013	North Poleline	Control	0.235	23.03	8.7	0.85	13	89	2797	597	1315	18	353	2.4	6.5
2013	North Poleline	Control	0.399	34.80	8.8	1.21	20	64	4862	840	982	16	107	2.6	7.5
2013	North Poleline	Control	0.363	41.68	8.7	1.32	17	65	6526	686	828	19	112	2.4	7.0
2013	North Poleline	Control	0.639	42.20	8.8	2.21	37	119	6021	734	1872	19	88	8.0	6.3
2013	North Poleline	Control	0.376	39.14	9.0	1.03	18	63	5650	631	1801	16	131	3.0	6.1
2013	North Poleline	GRSP Removed	0.354	43.94	9.1	1.19	29	75	6261	875	1658	19	33	9.7	6.5
2013	North Poleline	GRSP Removed	0.280	24.22	9.1	0.98	23	77	2930	724	1129	20	211	3.1	3.3
2013	North Poleline	GRSP Removed	0.594	37.42	8.6	0.91	12	42	6199	433	664	16	141	0.5	2.8
2013	North Poleline	GRSP Removed	0.242	29.32	8.8	0.68	16	63	4220	558	1061	21	208	3.4	9.6
2013	North Poleline	GRSP Removed	0.339	29.95	8.6	0.83	28	51	4915	374	519	21	101	1.6	7.2

Soil nutrients															
Year	Site	Group	Dry Gravimetric Weight (%)	Total Exchange Capacity (meq/100 g)	pH	Organic Matter (%)	S (ppm)	P (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	Al (mg/kg)	NO <sub>3</sub> (ppm)	NH <sub>4</sub> (ppm)
2013	North Poleline	GRSP Removed	0.445	30.80	8.8	1.07	15	56	4272	584	1447	14	272	1.1	6.1
2013	North Poleline	GRSP Removed	0.250	27.43	8.6	1.56	15	68	4052	528	752	18	345	9.0	3.6
2013	North Poleline	GRSP Removed	0.576	26.42	8.4	2.78	17	39	4156	373	644	20	239	3.3	7.4
2013	North Poleline	YUBR Removed	0.349	25.31	8.8	0.70	12	50	3470	587	911	17	309	0.8	5.1
2013	North Poleline	YUBR Removed	0.241	16.61	8.6	0.49	6	60	2278	398	534	16	280	0.7	7.5
2013	North Poleline	YUBR Removed	0.306	34.02	8.9	1.17	22	66	4743	795	1071	19	97	4.8	4.4
2013	North Poleline	YUBR Removed	0.477	28.50	8.9	0.87	12	51	3871	586	1357	15	337	2.8	7.8
2013	North Poleline	YUBR Removed	0.809	56.71	9.2	1.57	24	52	8290	1060	1989	19	55	5.1	2.7
2013	North Poleline	YUBR Removed	0.548	39.30	8.5	0.97	14	31	6284	533	861	21	122	1.3	7.5
2013	North Poleline	YUBR Removed	0.554	48.71	9.1	1.19	26	79	6809	1074	1760	19	60	4.4	7.0
2013	North Poleline	YUBR Removed	0.511	60.63	9.2	1.71	39	97	9345	919	1881	20	25	5.0	1.8
2013	Point of Rock	Control	0.005	17.82	8.3	1.28	29	97	2406	382	766	21	362	32.5	3.7
2013	Point of Rock	Control	0.006	14.16	8.6	0.61	8	64	1534	533	612	18	346	0.8	3.0
2013	Point of Rock	Control	0.039	11.92	8.2	0.47	7	117	1236	447	607	18	398	4.7	3.9

Year	Site	Group	Soil nutrients												
			Dry Gravimetric Weight (%)	Total Exchange Capacity (meq/100 g)	pH	Organic Matter (%)	S (ppm)	P (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	Al (mg/kg)	NO <sub>3</sub> (ppm)	NH <sub>4</sub> (ppm)
2013	Point of Rock	Control	0.054	12.63	8.4	0.72	11	125	1132	454	1071	14	389	10.8	2.8
2013	Point of Rock	Control	0.006	13.52	8.8	0.70	8	81	1297	505	937	16	362	1.7	3.5
2013	Point of Rock	Control	0.015	11.46	8.5	0.55	7	99	1003	473	822	15	361	2.0	3.1
2013	Point of Rock	Control	0.012	13.08	8.5	0.46	7	113	1503	427	604	17	430	3.0	2.4
2013	Point of Rock	Control	0.004	28.26	8.9	0.97	30	64	3921	606	1101	18	224	1.4	3.0
2013	Point of Rock	GRSP Removed	0.004	23.81	8.9	1.15	33	87	2781	755	1142	21	266	5.8	2.2
2013	Point of Rock	GRSP Removed	0.037	10.77	7.7	0.72	6	72	1004	461	561	16	369	5.5	3.9
2013	Point of Rock	GRSP Removed	0.010	20.33	8.9	0.72	13	68	2465	582	1005	17	277	2.8	4.3
2013	Point of Rock	GRSP Removed	0.017	15.81	8.6	0.76	10	64	1731	541	828	19	354	1.7	3.9
2013	Point of Rock	GRSP Removed	0.003	21.43	8.5	1.18	22	73	3050	468	613	19	303	6.6	8.8
2013	Point of Rock	GRSP Removed	0.005	22.57	8.7	0.98	15	60	2797	690	835	19	332	2.2	3.8
2013	Point of Rock	GRSP Removed	0.011	38.91	8.9	0.84	20	65	6021	562	1204	15	111	3.4	3.7
2013	Point of Rock	GRSP Removed	0.006	16.63	8.9	0.77	11	71	1515	647	1239	17	322	4.4	1.9
2013	Point of Rock	YUBR Removed	0.004	18.60	8.6	0.77	9	52	2638	389	611	19	338	0.5	4.6

Soil nutrients															
Year	Site	Group	Dry Gravimetric Weight (%)	Total Exchange Capacity (meq/100 g)	pH	Organic Matter (%)	S (ppm)	P (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	Al (mg/kg)	NO <sub>3</sub> (ppm)	NH <sub>4</sub> (ppm)
2013	Point of Rock	YUBR Removed	0.003	20.39	8.9	0.95	17	57	2218	609	1420	18	321	7.8	4.3
2013	Point of Rock	YUBR Removed	0.009	26.66	8.8	0.64	13	56	3877	554	737	17	239	1.2	4.6
2013	Point of Rock	YUBR Removed	0.006	25.46	8.9	0.89	17	69	2983	806	1213	19	254	3.0	3.9
2013	Point of Rock	YUBR Removed	0.014	13.19	8.8	0.44	11	77	1490	364	899	13	308	3.3	3.5
2013	Point of Rock	YUBR Removed	0.041	11.18	8.0	0.93	10	93	1178	378	658	17	350	10.7	3.8
2013	Point of Rock	YUBR Removed	0.010	20.76	8.9	0.88	24	74	2209	674	1363	20	275	7.3	3.4
2013	Point of Rock	YUBR Removed	0.004	19.10	9.2	1.11	23	100	1718	698	1635	19	291	8.0	1.0
2014	North Poleline	Control	0.867	26.28	8.6	0.69	15	57	3960	520	523	15	231	1.0	2.2
2014	North Poleline	Control	0.548	27.13	8.7	1.02	22	83	3612	748	784	21	199	8.7	2.1
2014	North Poleline	Control	0.398	28.49	8.9	1.04	21	108	4225	610	580	18	128	2.6	2.3
2014	North Poleline	Control	0.600	21.47	8.5	0.94	11	94	2781	558	865	17	346	3.8	2.0
2014	North Poleline	Control	0.775	33.02	8.7	1.45	21	83	4472	872	943	19	120	12.5	0.7
2014	North Poleline	Control	1.016	55.59	8.7	1.77	18	82	8810	941	828	16	75	2.3	0.4
2014	North Poleline	Control	1.274	51.75	9.0	2.48	43	158	7460	924	2121	17	65	9.2	1.6

Soil nutrients															
Year	Site	Group	Dry Gravimetric Weight (%)	Total Exchange Capacity (meq/100 g)	pH	Organic Matter (%)	S (ppm)	P (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	Al (mg/kg)	NO <sub>3</sub> (ppm)	NH <sub>4</sub> (ppm)
2014	North Poleline	Control	0.827	52.14	8.8	1.77	33	81	8198	787	1233	18	35	3.8	0.8
2014	North Poleline	GRSP Removed	0.521	36.12	8.7	1.07	23	79	5102	752	1278	20	92	23.2	3.0
2014	North Poleline	GRSP Removed	0.595	28.63	8.8	0.69	13	43	3959	630	1080	16	199	8.0	5.4
2014	North Poleline	GRSP Removed	0.970	29.18	8.5	0.88	12	50	4731	376	577	15	246	4.4	2.4
2014	North Poleline	GRSP Removed	0.572	27.13	8.9	0.59	14	61	3915	520	966	15	202	4.2	1.4
2014	North Poleline	GRSP Removed	0.829	24.99	8.8	0.80	16	49	3865	411	590	18	202	2.8	2.1
2014	North Poleline	GRSP Removed	1.546	34.72	8.7	1.31	22	80	4819	762	1266	20	162	3.8	2.1
2014	North Poleline	GRSP Removed	0.696	42.62	9.1	1.62	19	77	5774	1084	1426	18	84	13.7	2.7
2014	North Poleline	GRSP Removed	0.412	35.22	8.4	0.97	10	43	6044	330	440	15	168	2.7	2.9
2014	North Poleline	YUBR Removed	0.689	30.70	9.0	1.04	22	75	3803	908	1285	20	183	6.1	2.8
2014	North Poleline	YUBR Removed	1.053	27.25	9.0	0.78	16	60	3545	724	1079	16	236	6.2	2.9
2014	North Poleline	YUBR Removed	0.766	31.85	8.6	1.09	24	66	4617	667	866	21	114	10.8	3.1
2014	North Poleline	YUBR Removed	1.220	29.74	8.7	0.91	13	55	4207	587	1149	14	271	4.3	1.3
2014	North Poleline	YUBR Removed	1.462	67.24	9.5	2.27	30	59	10049	1287	1914	20	37	7.3	1.6

Soil nutrients															
Year	Site	Group	Dry Gravimetric Weight (%)	Total Exchange Capacity (meq/100 g)	pH	Organic Matter (%)	S (ppm)	P (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	Al (mg/kg)	NO <sub>3</sub> (ppm)	NH <sub>4</sub> (ppm)
2014	North Poleline	YUBR Removed	1.076	35.15	8.7	1.41	21	48	5068	682	1209	17	182	8.0	1.0
2014	North Poleline	YUBR Removed	1.667	41.37	8.8	1.18	17	66	5803	924	1369	16	115	2.6	1.9
2014	North Poleline	YUBR Removed	1.053	50.57	8.9	2.37	41	91	7830	792	1352	20	39	11.1	1.2
2014	Point of Rock	Control	0.968	22.99	8.5	1.03	17	88	3149	462	1032	19	401	7.6	1.9
2014	Point of Rock	Control	1.532	18.52	8.6	0.42	7	42	2520	441	650	14	341	1.2	1.8
2014	Point of Rock	Control	0.758	13.02	8.5	1.04	14	71	1378	483	645	18	283	6.2	4.3
2014	Point of Rock	Control	0.641	13.44	8.6	0.79	9	112	1206	504	1079	15	376	4.3	3.7
2014	Point of Rock	Control	1.812	14.65	8.8	0.64	8	70	1352	555	1100	15	331	1.1	3.8
2014	Point of Rock	Control	0.527	11.94	8.5	0.50	6	104	1037	481	909	15	382	2.1	3.6
2014	Point of Rock	Control	0.919	13.31	8.6	0.62	7	110	1534	434	620	15	401	2.3	3.2
2014	Point of Rock	Control	1.419	29.31	8.7	0.99	19	61	4076	606	1174	17	248	1.2	3.4
2014	Point of Rock	GRSP Removed	1.740	17.59	8.6	0.78	12	56	1968	633	743	18	310	4.8	2.5
2014	Point of Rock	GRSP Removed	1.463	12.85	8.0	0.67	5	60	1128	631	567	15	434	2.5	2.2
2014	Point of Rock	GRSP Removed	1.160	26.03	9.5	0.77	33	65	2766	802	1927	18	206	11.1	2.5

Soil nutrients															
Year	Site	Group	Dry Gravimetric Weight (%)	Total Exchange Capacity (meq/100 g)	pH	Organic Matter (%)	S (ppm)	P (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	Al (mg/kg)	NO <sub>3</sub> (ppm)	NH <sub>4</sub> (ppm)
2014	Point of Rock	GRSP Removed	0.984	20.88	8.6	0.99	22	68	2421	656	1029	19	268	11.1	3.5
2014	Point of Rock	GRSP Removed	0.521	26.18	8.8	2.10	22	97	3093	854	1104	19	272	9.0	4.9
2014	Point of Rock	GRSP Removed	1.185	20.67	8.8	1.14	14	56	2420	657	968	17	337	7.5	4.2
2014	Point of Rock	GRSP Removed	2.060	31.78	8.7	0.91	17	66	4919	489	852	16	166	3.4	3.2
2014	Point of Rock	GRSP Removed	1.284	20.66	9.1	0.85	12	75	1669	864	1764	26	342	3.6	3.1
2014	Point of Rock	YUBR Removed	1.464	26.11	8.7	1.17	27	70	3195	641	1562	20	305	10.6	1.5
2014	Point of Rock	YUBR Removed	1.069	21.89	9.1	0.99	19	67	2123	805	1553	19	275	10.5	2.9
2014	Point of Rock	YUBR Removed	1.131	23.15	8.7	0.71	13	61	3101	633	650	19	294	1.0	1.5
2014	Point of Rock	YUBR Removed	0.921	24.34	8.8	0.87	14	78	2850	821	990	18	285	2.5	0.5
2014	Point of Rock	YUBR Removed	0.642	21.53	9.0	1.09	23	64	2690	541	1161	19	252	6.9	3.8
2014	Point of Rock	YUBR Removed	0.666	12.48	8.3	0.78	10	98	1251	447	792	18	361	4.0	3.8
2014	Point of Rock	YUBR Removed	1.000	22.42	8.8	0.86	33	71	2351	740	1497	18	242	21.3	3.5
2014	Point of Rock	YUBR Removed	0.865	21.31	8.9	1.23	54	91	1947	795	1686	22	267	34.3	3.0



Table 3.5: Results of leaf nutrient analysis. GRSP = *Grayia spinosa*; YUBR = *Yucca brevifolia*

			Leaf nutrients												
Year	Site	Group	Species	N (%)	P (%)	Mg (%)	K (%)	Ca (%)	S (%)	B (ppm)	Fe (ppm)	Mn (ppm)	Cu (ppm)	Zn (ppm)	Al (ppm)
2013	North Poleline	Control	GRSP	1.05	0.059	1.860	7.93	2.78	0.427	73.5	92.0	162.0	1.3	8.8	137.0
2013	North Poleline	Control	YUBR	1.26	0.123	0.727	2.73	1.71	0.210	36.2	84.2	94.9	1.5	7.3	111.0
2013	North Poleline	Control	GRSP	0.85	0.064	1.430	6.09	2.56	0.365	57.6	99.3	138.0	1.2	5.1	128.0
2013	North Poleline	Control	YUBR	1.30	0.126	0.619	2.21	1.69	0.202	37.4	101.0	75.6	1.3	9.7	143.0
2013	North Poleline	Control	GRSP	0.82	0.053	1.060	4.60	2.81	0.296	58.1	72.0	156.0	1.1	2.8	106.0
2013	North Poleline	Control	YUBR	0.81	0.140	0.404	1.52	1.52	0.134	30.1	59.7	66.1	0.9	3.9	84.0
2013	North Poleline	Control	GRSP	1.27	0.062	1.800	8.01	3.03	0.496	79.0	77.8	68.3	1.3	4.2	107.0
2013	North Poleline	Control	YUBR	1.26	0.116	0.417	1.54	1.42	0.152	24.2	48.6	44.5	1.5	4.0	65.2
2013	North Poleline	Control	GRSP	0.74	0.040	2.470	5.61	4.07	0.458	69.7	117.0	115.0	1.4	4.8	168.0
2013	North Poleline	Control	YUBR	0.82	0.102	0.630	1.69	1.54	0.166	24.9	63.5	46.3	1.4	4.7	96.2
2013	North Poleline	Control	GRSP	0.75	0.053	1.950	6.70	3.54	0.615	98.9	99.2	86.6	1.7	4.8	153.0
2013	North Poleline	Control	YUBR	0.92	0.133	0.464	0.76	1.39	0.099	31.3	41.2	61.9	1.6	4.5	61.6
2013	North Poleline	Control	GRSP	1.45	0.063	2.410	8.11	4.27	0.600	64.6	79.2	133.0	1.6	4.1	134.0
2013	North Poleline	Control	YUBR	0.97	0.149	0.609	1.64	1.75	0.172	34.6	48.1	66.1	1.6	4.7	63.6
2013	North Poleline	Control	GRSP	0.89	0.065	1.110	7.45	4.21	0.509	76.7	60.1	122.0	1.2	5.3	116.0
2013	North Poleline	Control	YUBR	0.84	0.165	0.386	1.95	1.79	0.152	32.5	40.9	53.1	1.9	5.3	65.7
2013	North Poleline	GRSP Removed	YUBR	1.34	0.118	0.450	1.84	1.47	0.158	30.1	58.7	65.5	2.6	7.0	81.7
2013	North Poleline	GRSP Removed	YUBR	1.15	0.149	0.564	2.04	1.73	0.204	35.8	59.5	63.5	1.2	7.2	91.7
2013	North Poleline	GRSP Removed	YUBR	0.79	0.106	0.306	0.93	1.18	0.104	29.4	38.6	38.6	1.3	4.0	56.8
2013	North Poleline	GRSP Removed	YUBR	0.87	0.144	0.314	0.90	1.22	0.115	19.6	40.7	49.8	1.1	4.7	55.3
2013	North Poleline	GRSP Removed	YUBR	0.99	0.101	0.240	0.76	0.95	0.101	18.2	46.5	37.2	4.4	7.0	63.7
2013	North Poleline	GRSP Removed	YUBR	0.89	0.097	0.301	0.97	0.99	0.108	18.9	34.7	30.2	1.1	3.5	53.0
2013	North Poleline	GRSP Removed	YUBR	1.16	0.105	0.546	1.47	1.50	0.167	29.6	72.0	41.3	1.4	4.9	95.8
2013	North Poleline	GRSP Removed	YUBR	0.95	0.134	0.419	0.73	1.12	0.108	34.9	41.8	47.8	3.5	6.2	52.7

Leaf nutrients															
Year	Site	Group	Species	N (%)	P (%)	Mg (%)	K (%)	Ca (%)	S (%)	B (ppm)	Fe (ppm)	Mn (ppm)	Cu (ppm)	Zn (ppm)	Al (ppm)
2013	North Poleline	YUBR Removed	GRSP	1.17	0.085	1.680	7.91	2.08	0.663	83.2	72.2	136.0	1.2	6.7	98.5
2013	North Poleline	YUBR Removed	GRSP	1.07	0.063	1.320	5.49	2.46	0.272	63.4	66.8	157.0	1.1	3.8	96.0
2013	North Poleline	YUBR Removed	GRSP	0.78	0.050	1.540	6.55	2.13	0.537	67.8	84.5	122.0	1.1	3.5	113.0
2013	North Poleline	YUBR Removed	GRSP	0.85	0.047	1.700	6.82	2.84	0.610	78.0	56.3	131.0	1.0	3.9	104.0
2013	North Poleline	YUBR Removed	GRSP	1.08	0.048	1.670	7.04	5.59	0.500	63.5	85.3	117.0	1.4	4.2	131.0
2013	North Poleline	YUBR Removed	GRSP	0.91	0.052	1.900	6.89	4.28	0.546	80.6	83.0	132.0	1.4	5.8	150.0
2013	North Poleline	YUBR Removed	GRSP	0.84	0.056	1.960	7.67	3.99	0.369	69.1	102.0	250.0	1.5	5.1	158.0
2013	North Poleline	YUBR Removed	GRSP	1.01	0.063	1.370	6.50	3.17	0.507	71.4	62.3	124.0	1.2	3.9	100.0
2013	Point of Rock	Control	GRSP	1.52	0.062	2.240	10.60	2.12	0.529	112.0	117.0	160.0	1.7	5.9	147.0
2013	Point of Rock	Control	YUBR	1.57	0.168	0.682	2.75	1.45	0.216	53.0	99.8	86.8	1.6	6.4	131.0
2013	Point of Rock	Control	GRSP	1.36	0.109	2.290	6.68	2.23	1.030	154.0	164.0	83.7	1.8	4.5	158.0
2013	Point of Rock	Control	YUBR	1.41	0.139	1.010	3.50	1.50	0.434	75.7	115.0	67.5	2.2	6.3	162.0
2013	Point of Rock	Control	GRSP	1.07	0.119	2.220	5.33	2.10	0.806	101.0	140.0	196.0	2.7	6.2	171.0
2013	Point of Rock	Control	YUBR	1.23	0.139	0.671	2.70	1.26	0.253	46.6	104.0	88.9	1.7	6.7	135.0
2013	Point of Rock	Control	GRSP	1.22	0.124	1.540	8.38	1.52	0.866	90.3	103.0	102.0	1.3	5.4	140.0
2013	Point of Rock	Control	YUBR	1.21	0.177	0.383	1.11	1.03	0.132	24.6	65.6	56.9	2.4	9.6	83.2
2013	Point of Rock	Control	GRSP	1.11	0.104	1.780	7.73	1.98	0.954	106.0	136.0	31.7	1.7	5.9	180.0
2013	Point of Rock	Control	YUBR	1.11	0.128	0.353	0.67	1.14	0.088	25.4	41.0	82.6	1.0	3.1	58.3
2013	Point of Rock	Control	GRSP	1.06	0.127	2.330	7.42	2.39	1.100	82.7	113.0	198.0	1.4	4.5	157.0
2013	Point of Rock	Control	YUBR	1.00	0.165	0.292	0.94	1.19	0.107	32.5	59.5	83.9	1.4	4.1	75.2
2013	Point of Rock	Control	GRSP	1.04	0.087	1.880	7.45	1.90	0.684	130.0	116.0	127.0	1.4	3.5	151.0
2013	Point of Rock	Control	YUBR	1.01	0.159	0.307	0.87	1.15	0.095	28.4	46.4	65.5	1.3	3.9	60.3
2013	Point of Rock	Control	GRSP	1.23	0.058	1.920	7.38	3.24	0.818	85.5	105.0	78.6	1.2	4.4	145.0
2013	Point of Rock	Control	YUBR	1.20	0.197	0.346	0.86	1.49	0.126	27.7	48.2	39.4	4.4	8.5	70.9
2013	Point of Rock	GRSP Removed	YUBR	1.58	0.203	0.438	1.30	1.17	0.159	25.0	60.0	54.6	1.9	6.1	76.2

Leaf nutrients															
Year	Site	Group	Species	N (%)	P (%)	Mg (%)	K (%)	Ca (%)	S (%)	B (ppm)	Fe (ppm)	Mn (ppm)	Cu (ppm)	Zn (ppm)	Al (ppm)
2013	Point of Rock	GRSP Removed	YUBR	1.16	0.195	0.454	1.08	1.22	0.131	36.4	54.3	77.0	17.7	16.7	65.4
2013	Point of Rock	GRSP Removed	YUBR	1.10	0.168	0.546	1.25	1.93	0.153	26.5	72.0	53.7	2.1	7.2	98.7
2013	Point of Rock	GRSP Removed	YUBR	1.15	0.133	0.427	1.41	0.97	0.165	29.1	55.5	62.6	2.6	6.9	74.8
2013	Point of Rock	GRSP Removed	YUBR	1.17	0.152	0.306	0.91	1.29	0.103	25.1	37.1	46.8	1.3	5.3	51.9
2013	Point of Rock	GRSP Removed	YUBR	1.06	0.164	0.397	0.97	1.73	0.127	39.1	62.5	59.2	2.4	5.5	94.8
2013	Point of Rock	GRSP Removed	YUBR	1.12	0.181	0.236	1.05	1.26	0.107	27.0	39.1	19.6	1.9	6.1	52.4
2013	Point of Rock	GRSP Removed	YUBR	1.12	0.173	0.262	1.02	0.93	0.094	20.7	31.6	41.1	2.0	7.2	42.1
2013	Point of Rock	YUBR Removed	GRSP	1.20	0.081	1.510	7.05	1.85	0.682	88.0	124.0	80.5	1.3	4.8	168.0
2013	Point of Rock	YUBR Removed	GRSP	1.55	0.068	1.740	9.86	1.74	0.566	95.9	112.0	134.0	1.6	4.8	149.0
2013	Point of Rock	YUBR Removed	GRSP	1.36	0.102	0.726	2.25	1.11	0.297	45.4	38.0	35.5	9.7	8.7	71.2
2013	Point of Rock	YUBR Removed	GRSP	1.35	0.097	2.530	6.39	2.09	0.857	65.4	121.0	74.9	1.9	5.2	148.0
2013	Point of Rock	YUBR Removed	GRSP	1.30	0.123	1.580	7.05	1.72	0.620	141.0	97.6	120.0	1.8	8.5	120.0
2013	Point of Rock	YUBR Removed	GRSP	1.13	0.121	1.490	7.69	1.79	0.612	106.0	137.0	117.0	1.8	6.8	167.0
2013	Point of Rock	YUBR Removed	GRSP	1.17	0.114	1.940	7.56	2.04	0.852	86.5	97.3	127.0	1.8	5.2	135.0
2013	Point of Rock	YUBR Removed	GRSP	1.10	0.097	1.970	10.40	1.67	0.637	73.6	97.2	133.0	1.6	4.4	118.0
2014	North Poleline	Control	GRSP	1.31	0.066	1.430	8.08	2.24	0.342	55.9	108.0	202.0	1.3	10.8	138.0
2014	North Poleline	Control	YUBR	1.38	0.168	0.472	2.06	1.22	0.174	22.1	94.8	76.4	1.7	7.3	120.0
2014	North Poleline	Control	GRSP	1.16	0.073	1.210	7.76	1.99	0.308	42.1	113.0	206.0	1.2	9.1	134.0
2014	North Poleline	Control	YUBR	1.19	0.126	0.438	1.24	1.52	0.146	24.0	64.5	69.7	1.3	5.8	87.4
2014	North Poleline	Control	GRSP	0.94	0.060	0.767	4.83	1.72	0.296	35.2	134.0	130.0	1.6	4.6	158.0
2014	North Poleline	Control	YUBR	0.97	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2014	North Poleline	Control	GRSP	0.64	0.100	0.498	2.44	1.24	0.144	23.6	44.9	49.1	1.2	4.1	63.2
2014	North Poleline	Control	YUBR	0.77	0.119	0.312	1.21	1.13	0.118	15.9	53.3	46.1	11.4	6.9	69.8
2014	North Poleline	Control	GRSP	0.87	0.088	0.875	3.47	1.81	0.151	26.0	55.4	87.7	1.5	5.3	82.9
2014	North Poleline	Control	YUBR	1.21	0.111	0.462	1.68	1.15	0.127	15.6	50.7	49.5	1.5	8.6	70.9

Leaf nutrients															
Year	Site	Group	Species	N (%)	P (%)	Mg (%)	K (%)	Ca (%)	S (%)	B (ppm)	Fe (ppm)	Mn (ppm)	Cu (ppm)	Zn (ppm)	Al (ppm)
2014	North Poleline	Control	GRSP	1.06	0.086	0.869	4.40	1.76	0.295	37.3	67.7	55.1	1.3	4.8	94.0
2014	North Poleline	Control	YUBR	1.19	0.146	0.468	0.77	1.32	0.112	28.4	43.7	54.1	1.8	12.2	50.8
2014	North Poleline	Control	GRSP	1.78	0.068	1.680	9.17	3.14	0.375	42.3	82.7	176.0	1.2	9.4	117.0
2014	North Poleline	Control	YUBR	1.55	0.140	0.640	2.25	1.66	0.184	29.5	72.7	77.3	1.1	5.4	94.4
2014	North Poleline	Control	GRSP	1.43	0.077	1.170	9.46	3.21	0.296	49.7	68.8	163.0	1.2	11.0	103.0
2014	North Poleline	Control	YUBR	1.41	0.116	0.469	2.69	1.77	0.169	27.8	64.2	75.5	1.5	6.2	80.9
2014	North Poleline	GRSP Removed	YUBR	1.39	0.138	0.230	0.77	1.04	0.122	17.9	83.7	108.0	2.0	8.0	97.5
2014	North Poleline	GRSP Removed	YUBR	1.17	0.134	0.453	1.59	1.72	0.151	26.9	63.4	72.5	1.3	4.8	80.6
2014	North Poleline	GRSP Removed	YUBR	0.91	0.125	0.339	0.93	1.55	0.112	20.2	64.0	59.9	1.3	4.7	79.4
2014	North Poleline	GRSP Removed	YUBR	0.95	0.128	0.332	1.23	1.29	0.119	18.7	71.5	59.0	1.3	4.6	104.0
2014	North Poleline	GRSP Removed	YUBR	0.88	0.138	0.294	0.74	1.21	0.108	15.7	39.3	38.5	1.7	4.3	53.1
2014	North Poleline	GRSP Removed	YUBR	1.14	0.111	0.408	1.73	1.43	0.156	20.6	82.9	49.9	2.6	6.5	135.0
2014	North Poleline	GRSP Removed	YUBR	0.92	0.140	0.434	0.80	1.18	0.102	17.8	44.4	37.3	1.1	4.1	56.3
2014	North Poleline	GRSP Removed	YUBR	0.86	0.105	0.357	0.58	0.94	0.085	20.4	38.5	31.0	1.3	3.6	53.6
2014	North Poleline	YUBR Removed	GRSP	1.36	0.083	1.000	5.69	1.65	0.305	48.4	70.4	89.1	1.4	5.8	91.0
2014	North Poleline	YUBR Removed	GRSP	0.84	0.071	0.690	3.65	1.40	0.107	30.2	54.6	104.0	0.9	4.7	75.1
2014	North Poleline	YUBR Removed	GRSP	1.14	0.064	1.230	5.59	1.81	0.293	38.5	78.5	145.0	1.2	6.5	113.0
2014	North Poleline	YUBR Removed	GRSP	1.76	0.087	1.400	8.61	2.42	0.552	56.9	73.2	131.0	1.9	8.0	106.0
2014	North Poleline	YUBR Removed	GRSP	0.78	0.070	0.668	3.53	1.63	0.218	25.7	42.9	50.5	1.0	4.8	64.8
2014	North Poleline	YUBR Removed	GRSP	1.25	0.059	1.610	8.51	2.85	0.451	62.7	111.0	124.0	1.7	8.8	148.0
2014	North Poleline	YUBR Removed	GRSP	1.18	0.062	1.590	8.52	3.13	0.356	57.5	91.5	358.0	1.8	9.0	136.0
2014	North Poleline	YUBR Removed	GRSP	1.23	0.065	1.500	9.13	3.39	0.274	56.3	71.1	242.0	1.0	6.2	106.0
2014	Point of Rock	Control	GRSP	1.30	0.089	0.637	4.61	1.18	0.162	31.9	56.7	80.6	1.3	5.2	80.1
2014	Point of Rock	Control	YUBR	1.58	0.149	0.546	2.83	1.50	0.181	34.1	76.0	73.9	1.7	6.5	94.1
2014	Point of Rock	Control	GRSP	2.00	0.142	1.370	9.02	1.86	0.388	77.2	100.0	108.0	2.4	12.6	135.0

Leaf nutrients															
Year	Site	Group	Species	N (%)	P (%)	Mg (%)	K (%)	Ca (%)	S (%)	B (ppm)	Fe (ppm)	Mn (ppm)	Cu (ppm)	Zn (ppm)	Al (ppm)
2014	Point of Rock	Control	YUBR	1.38	0.172	0.749	4.27	1.50	0.257	40.7	106.0	76.5	2.2	8.0	130.0
2014	Point of Rock	Control	GRSP	1.41	0.093	1.950	7.39	2.26	0.456	85.8	156.0	212.0	1.9	6.8	189.0
2014	Point of Rock	Control	YUBR	1.18	0.120	0.540	1.88	1.15	0.152	28.1	64.1	89.6	1.4	6.1	77.8
2014	Point of Rock	Control	GRSP	1.72	0.105	0.998	7.60	1.19	0.263	41.7	116.0	100.0	1.7	8.3	148.0
2014	Point of Rock	Control	YUBR	1.03	0.218	0.295	2.09	0.63	0.144	8.7	96.4	46.4	7.3	8.0	96.9
2014	Point of Rock	Control	GRSP	1.46	0.119	1.010	6.80	1.58	0.466	51.7	156.0	41.8	2.6	8.3	179.0
2014	Point of Rock	Control	YUBR	1.12	0.154	0.373	1.49	0.95	0.149	29.2	86.8	70.9	1.8	5.1	105.0
2014	Point of Rock	Control	GRSP	1.80	0.128	2.190	9.98	1.90	1.140	59.1	147.0	291.0	2.5	8.7	181.0
2014	Point of Rock	Control	YUBR	1.40	0.164	0.501	2.01	1.57	0.207	44.1	122.0	107.0	2.2	6.3	145.0
2014	Point of Rock	Control	GRSP	1.77	0.095	1.660	10.00	1.67	0.633	81.8	137.0	169.0	2.3	8.9	170.0
2014	Point of Rock	Control	YUBR	1.24	0.148	0.368	1.08	1.35	0.142	26.5	91.6	70.0	1.4	5.5	115.0
2014	Point of Rock	Control	GRSP	1.20	0.116	0.948	4.32	1.79	0.348	40.9	75.8	62.0	1.5	6.3	101.0
2014	Point of Rock	Control	YUBR	1.03	0.130	0.333	1.12	1.35	0.132	20.1	63.9	33.4	1.9	6.0	88.3
2014	Point of Rock	GRSP Removed	YUBR	1.42	0.213	0.404	1.38	1.35	0.146	22.0	50.2	62.4	1.5	5.2	62.0
2014	Point of Rock	GRSP Removed	YUBR	1.41	0.212	0.564	1.93	1.11	0.164	27.3	67.6	97.5	8.6	12.6	85.6
2014	Point of Rock	GRSP Removed	YUBR	1.36	0.151	0.588	2.77	1.57	0.174	29.6	57.3	95.7	1.9	7.7	65.9
2014	Point of Rock	GRSP Removed	YUBR	1.10	0.101	0.333	1.31	0.96	0.119	18.6	48.2	53.8	1.0	5.0	59.8
2014	Point of Rock	GRSP Removed	YUBR	1.39	0.149	0.296	1.01	1.25	0.123	21.7	62.3	61.9	1.9	5.5	73.7
2014	Point of Rock	GRSP Removed	YUBR	1.03	0.130	0.284	0.86	1.10	0.105	18.9	71.0	52.2	1.4	4.2	89.0
2014	Point of Rock	GRSP Removed	YUBR	1.13	0.158	0.195	1.16	1.12	0.102	21.3	41.2	19.7	1.5	5.2	56.5
2014	Point of Rock	GRSP Removed	YUBR	1.05	0.135	0.172	0.86	0.73	0.080	14.0	55.7	36.1	1.2	4.8	74.7
2014	Point of Rock	YUBR Removed	GRSP	1.92	0.116	1.110	7.92	1.52	0.458	52.1	110.0	93.6	2.2	11.3	131.0
2014	Point of Rock	YUBR Removed	GRSP	2.70	0.186	1.170	9.41	1.23	0.465	52.9	102.0	105.0	1.6	8.9	118.0
2014	Point of Rock	YUBR Removed	GRSP	1.26	0.109	0.871	5.48	1.81	0.294	43.4	96.8	69.2	1.1	5.8	131.0
2014	Point of Rock	YUBR Removed	GRSP	1.89	0.143	1.320	8.96	1.48	0.360	40.7	83.8	138.0	3.1	10.4	99.9

Leaf nutrients

Year	Site	Group	Species	N (%)	P (%)	Mg (%)	K (%)	Ca (%)	S (%)	B (ppm)	Fe (ppm)	Mn (ppm)	Cu (ppm)	Zn (ppm)	Al (ppm)
2014	Point of Rock	YUBR Removed	GRSP	1.62	0.098	1.060	7.15	1.29	0.363	62.2	84.1	65.2	1.6	7.5	103.0
2014	Point of Rock	YUBR Removed	GRSP	1.17	0.101	0.624	3.33	1.18	0.197	36.8	65.2	95.8	1.3	5.4	89.8
2014	Point of Rock	YUBR Removed	GRSP	1.42	0.115	1.160	6.33	1.76	0.427	44.7	104.0	165.0	2.1	7.2	138.0
2014	Point of Rock	YUBR Removed	GRSP	0.69	0.074	0.311	2.64	0.50	0.150	14.5	34.7	49.2	1.1	3.6	44.6

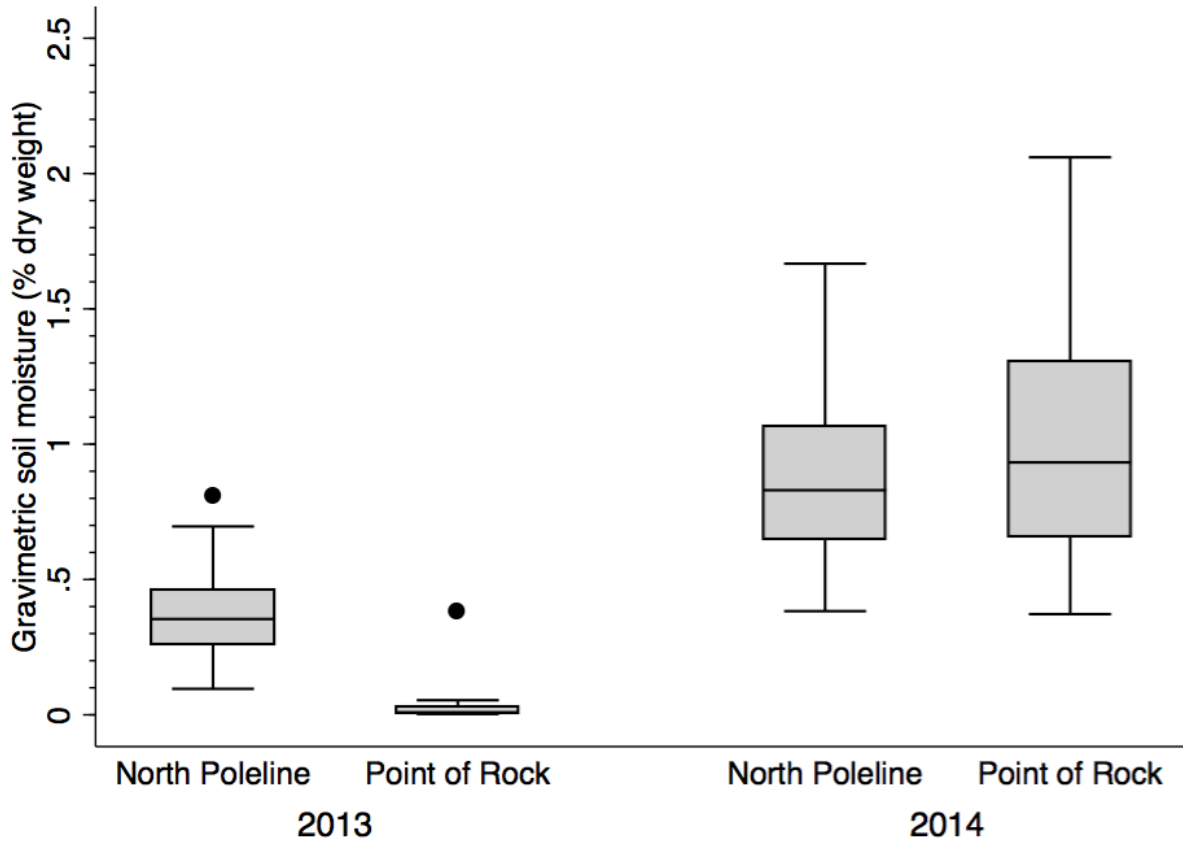


Figure 3.1: Gravimetric soil moisture by year and site.

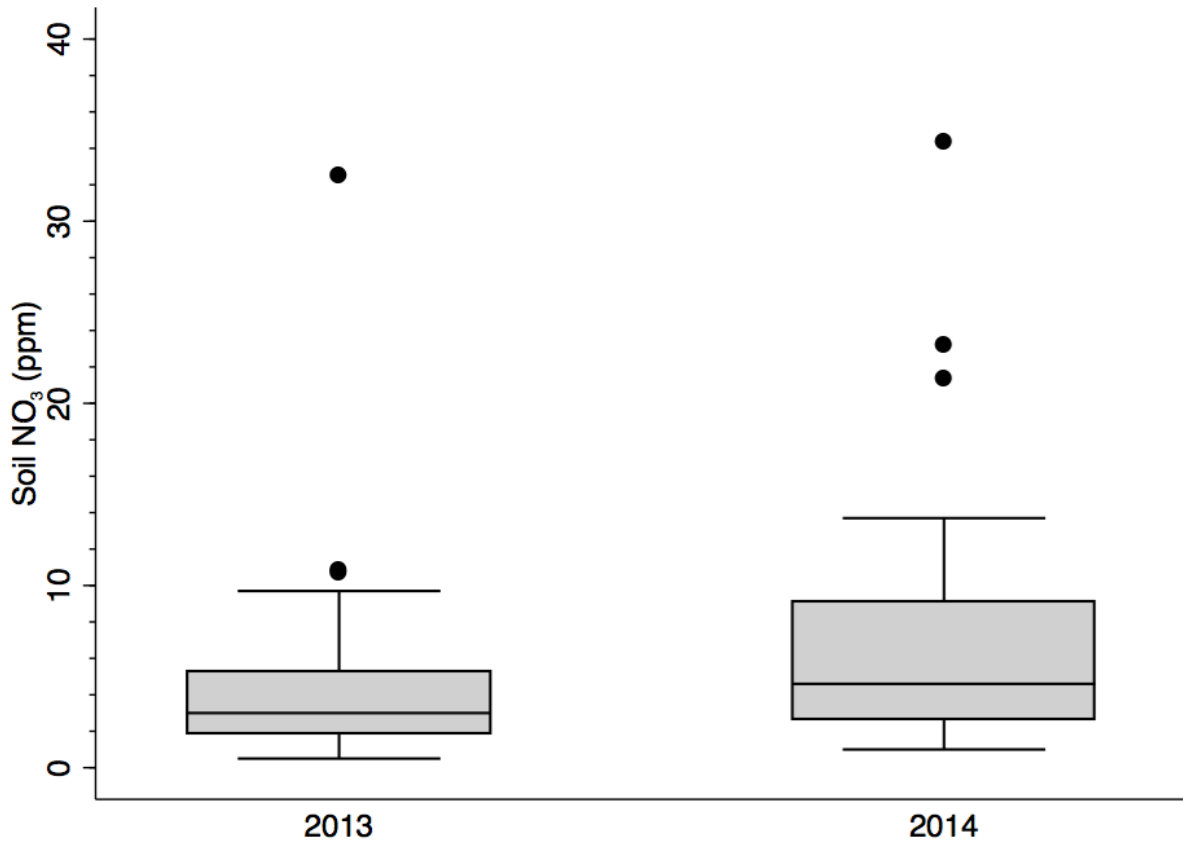


Figure 3.2: Soil NO<sub>3</sub> by year. The 'year' model was selected as the most parsimonious of the model set.



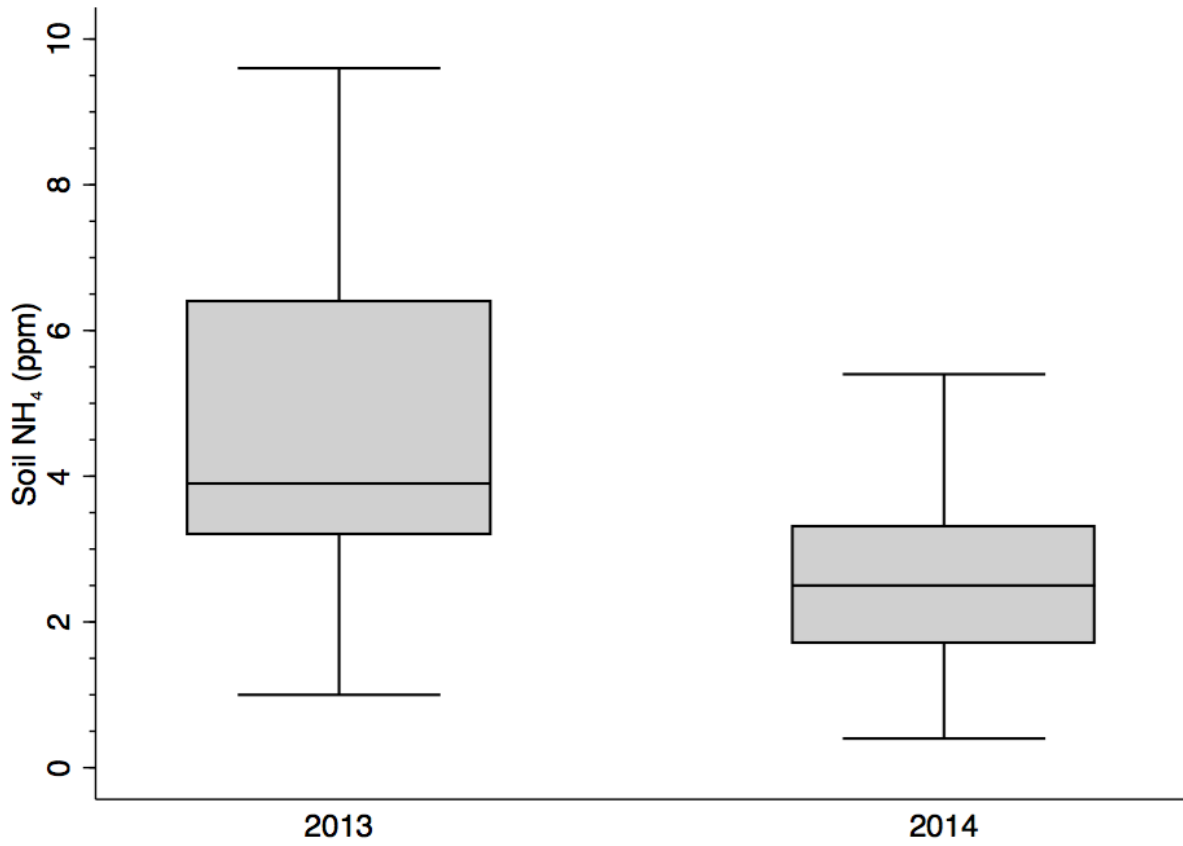


Figure 3.3: Soil NH<sub>4</sub> by year. The 'year' model was selected as the most parsimonious of the model set.

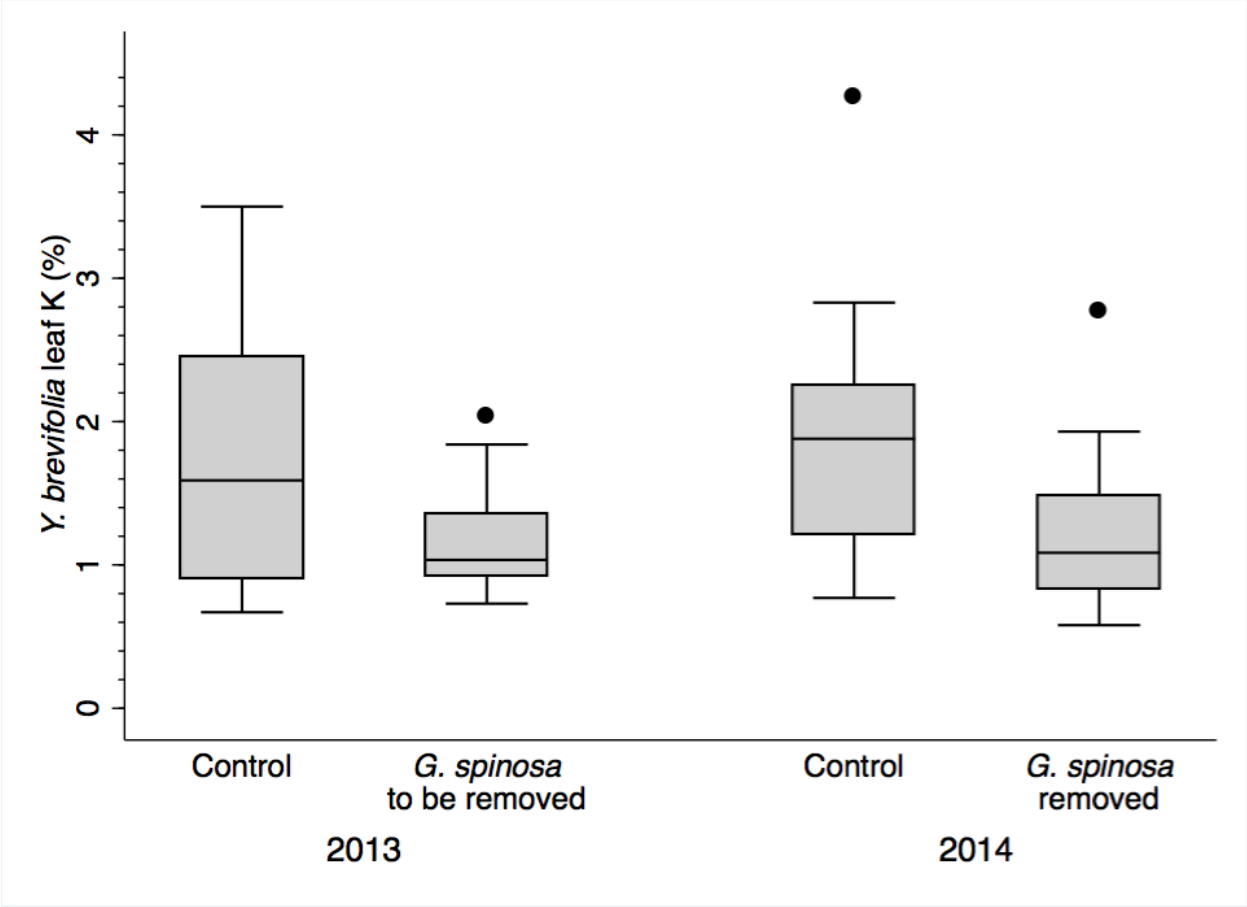


Figure 3.4: *Yucca brevifolia* leaf K by year and treatment. The 'treatment' model was selected as the most parsimonious of the model set. It should be noted that sampling in 2013 was conducted just prior to plant removal.

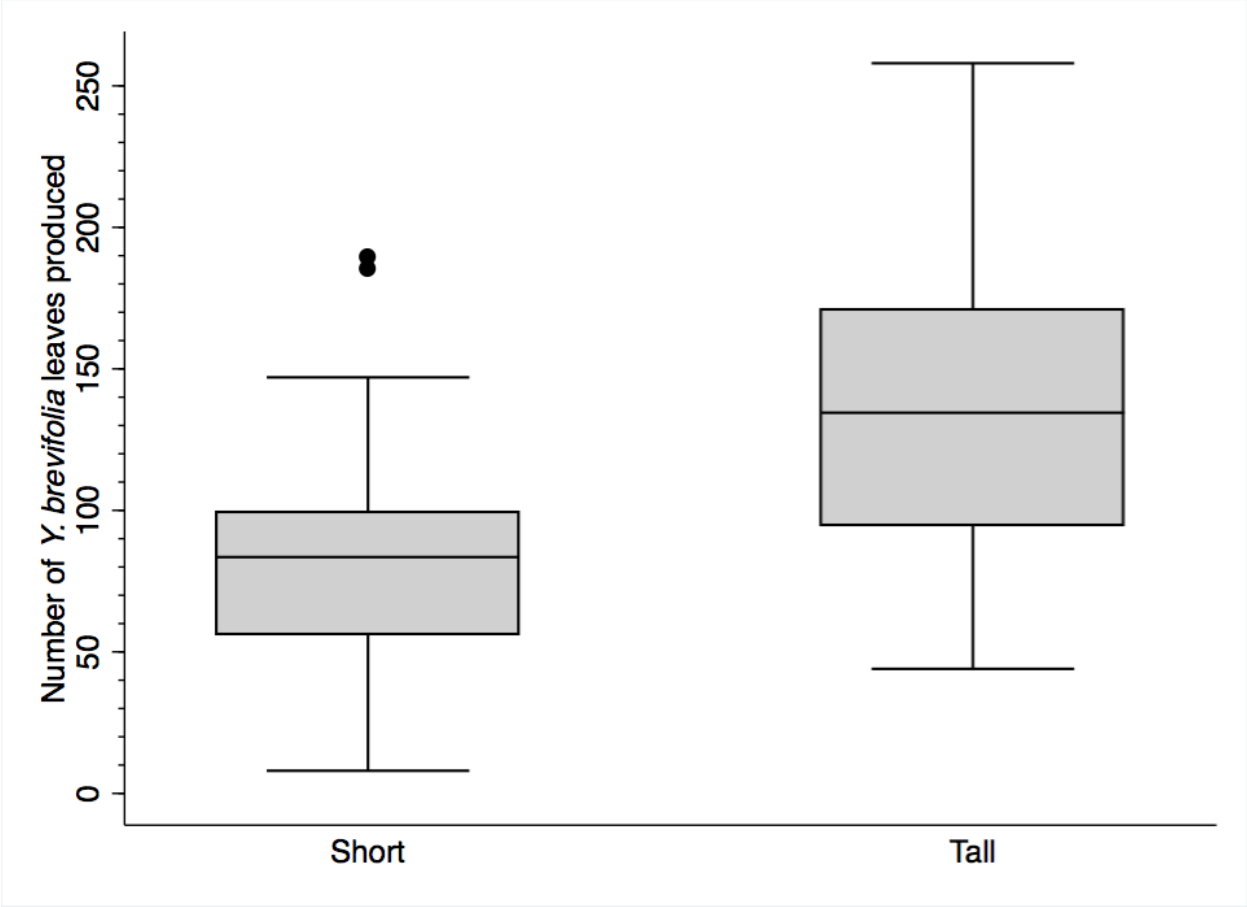


Figure 3.5: *Yucca brevifolia* leaf counts by height. The 'height' model was selected as the most parsimonious of the model set.

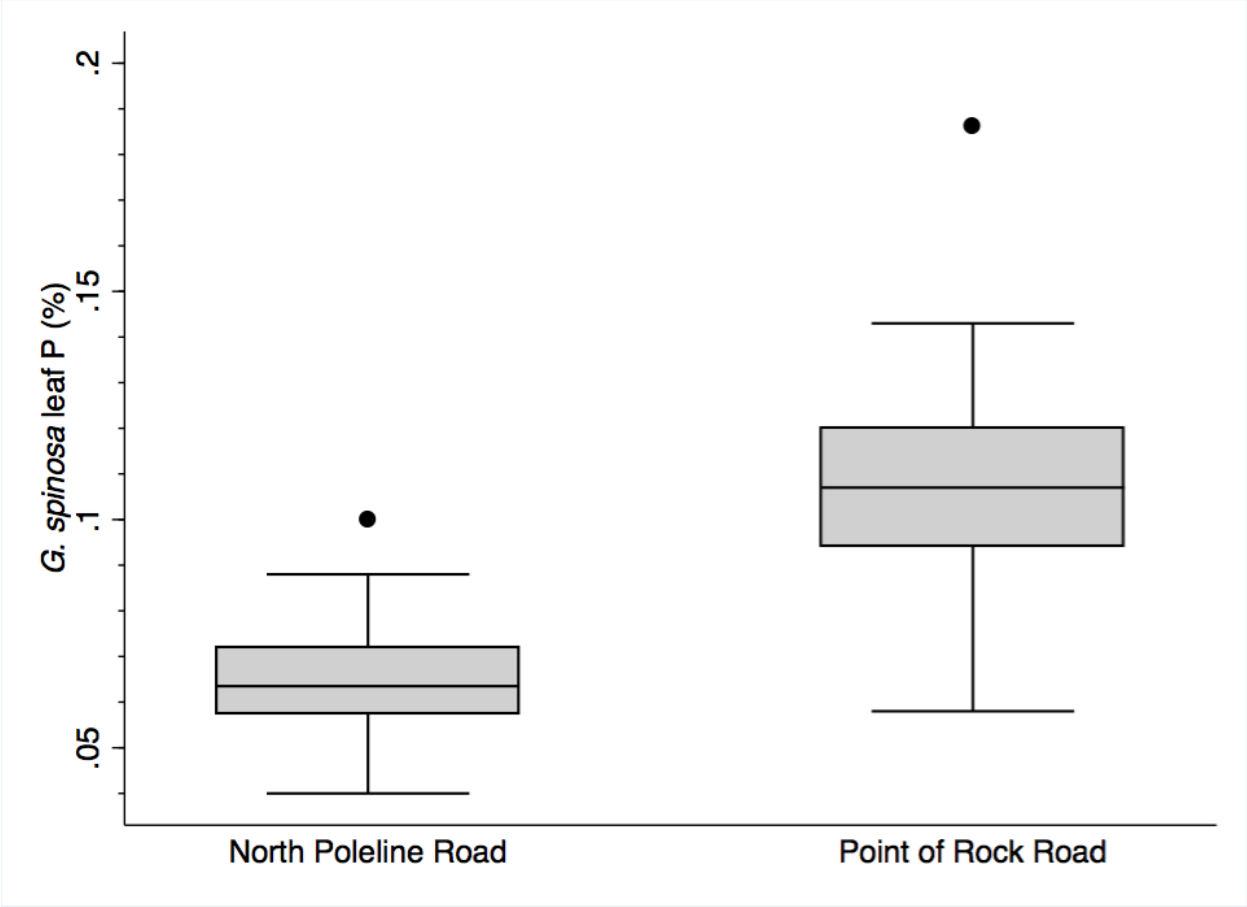


Figure 3.6: *Grayia spinosa* leaf P by site. The 'site' model was selected as the most parsimonious of the model set.

APPENDIX D:

TABLES AND FIGURES FOR CHAPTER 4

Table 4.1: AIC<sub>c</sub> results and rankings of models examining shrub species, relative height, and degree of exposure on herbivory leaf damage to *Y. brevifolia*.

Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	Δ AIC <sub>c</sub>	Akaike weight	Evidence ratio
Null	-360.64	2	723.41	7	49.36	0.00	5.23E+10
Shrub species ('species')	-355.47	3	719.20	5	45.15	0.00	6.37E+9
Degrees of exposure ('exposure')	-335.39	3	675.05	2	1.00	0.28	1.65
<i>Y. brevifolia</i> height:shrub height ('height')	-360.59	3	725.44	8	51.39	0.00	1.44E+11
<b>Species + exposure</b>	<b>-331.80</b>	<b>4</b>	<b>674.05</b>	<b>1</b>	<b>0.00</b>	<b>0.46</b>	<b>1.00</b>
Species + height	-355.42	4	721.27	6	47.22	0.00	1.79E+10
Exposure + height	-335.36	4	677.15	4	3.10	0.10	4.71
Species + exposure + height	-331.71	5	676.09	3	2.04	0.17	2.78

Table 4.2: AIC<sub>c</sub> results for models examining the effect of treatment on herbivory leaf damage to *Y. brevifolia* from 2014 to 2015.

Model description	Log likelihood	K	AIC <sub>c</sub>	Rank	$\Delta$ AIC <sub>c</sub>	Akaike weight	Evidence ratio
Null	-290.67	2	583.49	2	12.34	0.00	478.73
<b>Treatment</b>	<b>-283.43</b>	<b>3</b>	<b>571.15</b>	<b>1</b>	<b>0.00</b>	<b>1.00</b>	<b>1.00</b>

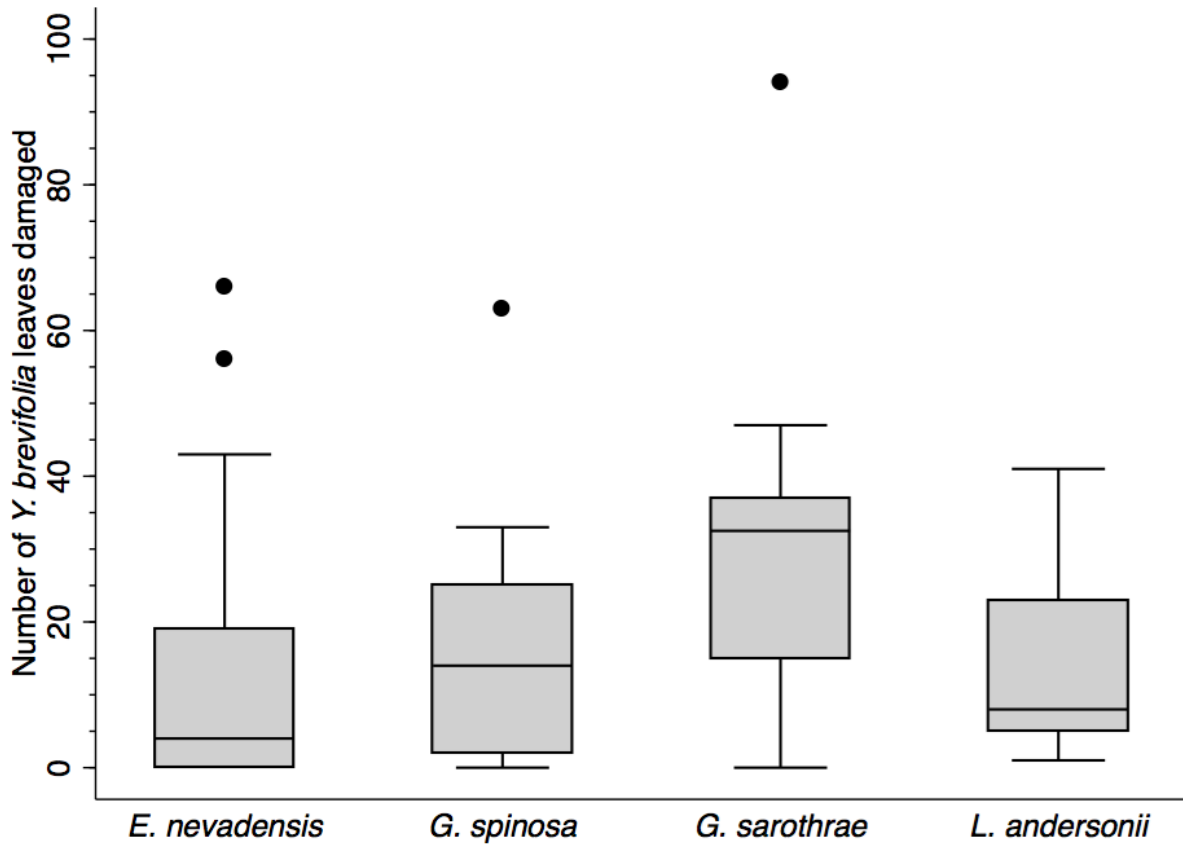


Figure 4.1: The number of *Y. brevifolia* leaves showing herbivore damage plotted by the four most recorded species of nurse shrub.

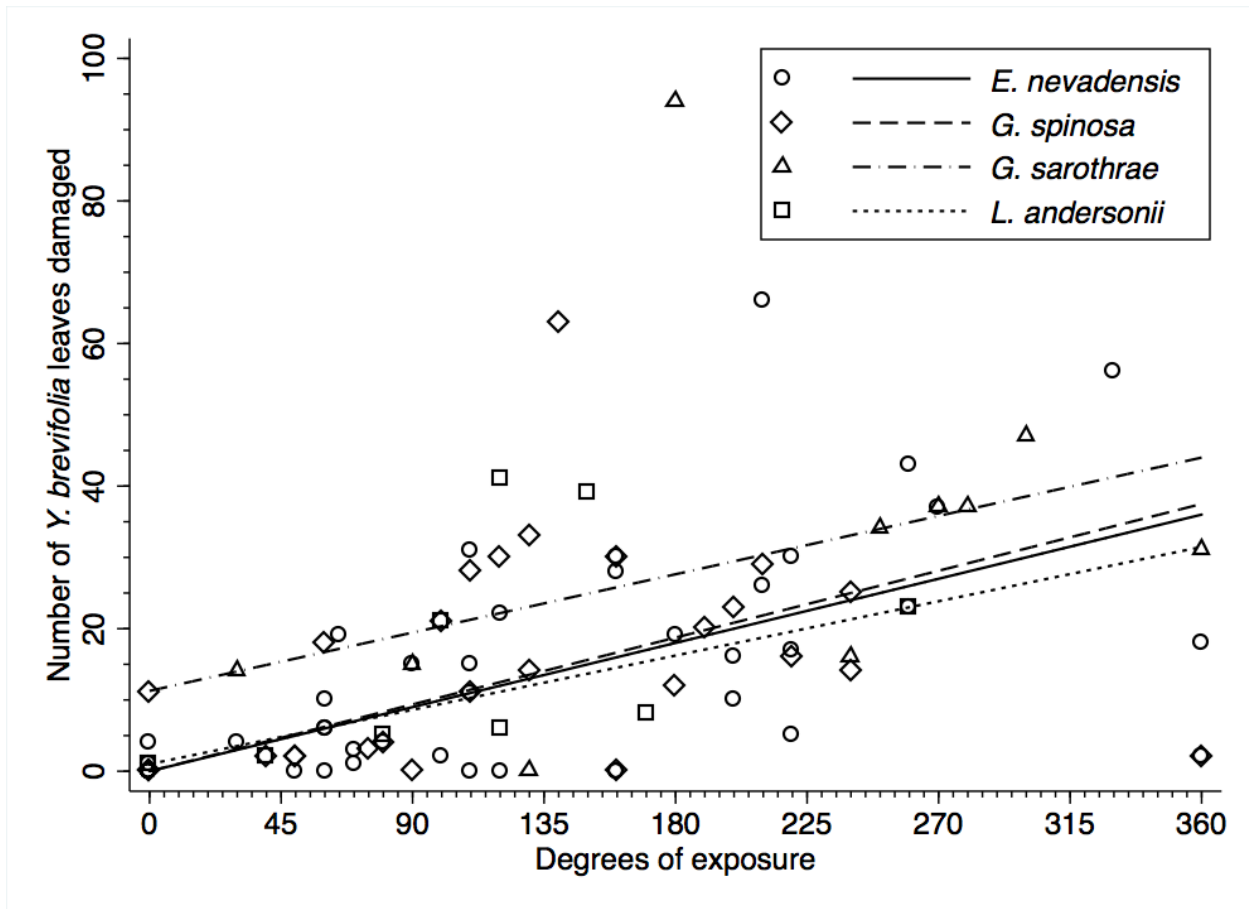


Figure 4.2: The number of *Y. brevifolia* leaves showing herbivore damage plotted by degrees of exposure and nurse plant species. The data is fitted with median regression lines for each nurse plant species: *E. nevadensis* ( $y = 0 + .1x$ ), *G. spinosa* ( $y = 0 + .1041667x$ ), *G. sarothrae* ( $y = 11.27273 + .0909091x$ ), and *L. andersonii* ( $y = 0 + .0846154x$ ).



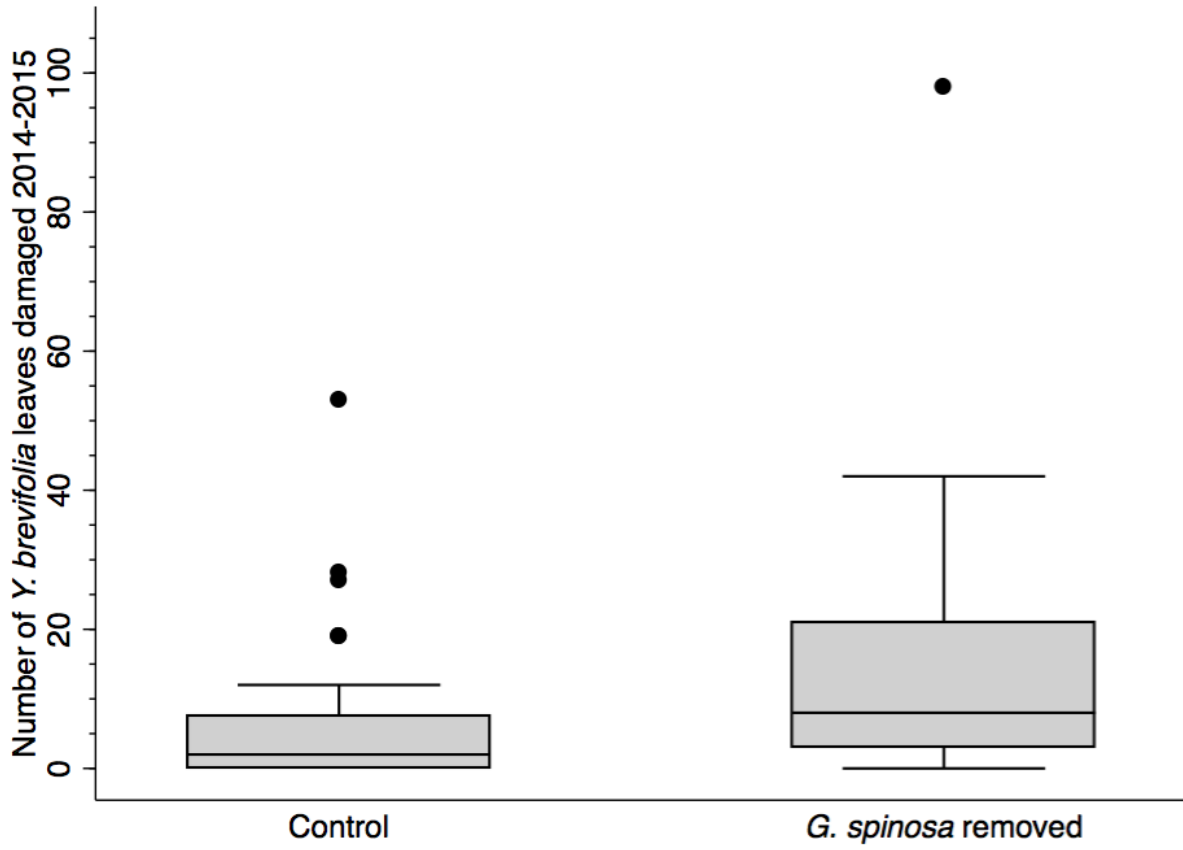


Figure 4.3: The number of herbivore damaged *Y. brevifolia* leaves by experimental group from 2014 to 2015.

## LITERATURE CITED

- Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. *The Journal of Wildlife Management* 66:912–918.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *The Journal of Wildlife Management* 74:1175–1178.
- Barbosa, P., J. Hines, I. Kaplan, H. Martinson, A. Szczepaniec, and Z. Szendrei. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. *Annual Review of Ecology, Evolution, and Systematics* 40:1–20.
- Barbour, M. G., J. H. Burk, W. D. Pitts, F. S. Gilliam, and M. W. Schwartz. 1998. *Terrestrial Plant Ecology*. Third edition. Benjamin Cummings.
- Barrows, C. W., and M. L. Murphy-Mariscal. 2012. Modeling impacts of climate change on Joshua trees at their southern boundary: how scale impacts predictions. *Biological Conservation* 152:29–36.
- Beatley, J. C. 1976. *Vascular plants of the Nevada Test Site and central-southern Nevada: ecologic and geographic distributions*. California Univ., Los Angeles (USA). Lab. of Nuclear Medicine and Radiation Biology.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* 9:191–193.
- Bonham, C. D. 2013. *Measurements for Terrestrial Vegetation*. John Wiley & Sons.
- Bowns, J. 1973, January 1. An Autecological Study of Blackbrush (*Coleogyne ramosissima* torr.) in Southwestern Utah.
- Brittingham, S., and L. R. Walker. 2000. Facilitation of *Yucca brevifolia* recruitment by Mojave Desert shrubs. *Western North American Naturalist* 60:374–383.
- Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, K. Tielbörger, J. M. J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket, S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. Pugnaire, C. L. Quiroz, P. Saccone, K. Schiffers, M. Seifan, B. Touzard, and R. Michalet. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96:18–34.
- Brussard, P., D. Charlet, D. Dobkin, L. Ball, K. Bishop, H. Britten, E. Fleishman, S. Fleury, T. Jenni, and T. Kennedy. 1998. Great Basin-Mojave Desert Region. Status and trends of the nation's biological resources. US Geological Survey 2.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Callaway, R. M. 1998. Are positive interactions species-specific? *Oikos* 82:202–207.

- Callaway, R. M. 2007. Positive Interactions and Interdependence in Plant Communities. Springer, Dordrecht.
- Callaway, R. M., Z. Kikvidze, and D. Kikodze. 2000. Facilitation by unpalatable weeds may conserve plant diversity in overgrazed meadows in the Caucasus Mountains. *Oikos* 89:275–282.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965.
- Chamberlin, T. C. 1965. The method of multiple working hypotheses. *Science* 148:754–759.
- Cody, M. 1986. Spacing patterns in Mojave Desert plant communities: near-neighbor analyses. *Journal of Arid Environments* 11:199–217.
- Cody, M. L. 2000. Slow-motion population dynamics in Mojave Desert perennial plants. *Journal of Vegetation Science* 11:351–358.
- Cole, K. L., K. Ironside, J. Eischeid, G. Garfin, P. B. Duffy, and C. Toney. 2010. Past and ongoing shifts in Joshua tree distribution support future modeled range contraction. *Ecological Applications* 21:137–149.
- Comanor, P. L., and W. H. Clark. 2000. Preliminary growth rates and a proposed age-form classification for the Joshua tree, *Yucca brevifolia* (Agavaceae). *Haseltonia* 7:37–46.
- Corlett, R. T., and D. A. Westcott. 2013. Will plant movements keep up with climate change? *Trends in Ecology & Evolution* 28:482–488.
- DeFalco, L. A., T. C. Esque, S. J. Scoles-Sciulla, and J. Rodgers. 2010. Desert wildfire and severe drought diminish survivorship of the long-lived Joshua tree (*Yucca brevifolia*; Agavaceae). *American Journal of Botany* 97:243–250.
- Drezner, T. D. 2006. Plant facilitation in extreme environments: The non-random distribution of saguaro cacti (*Carnegiea gigantea*) under their nurse associates and the relationship to nurse architecture. *Journal of Arid Environments* 65:46–61.
- Eakin, T. E. 1963. Ground-water Appraisal of Dry Lake and Delamar Valleys, Lincoln County, Nevada. Department of Conservation and Natural Resources.
- Elliott, L. P., and B. W. Brook. 2007. Revisiting Chamberlin: multiple working hypotheses for the 21st century. *BioScience* 57:608–614.
- Esque, T. C. 2003. Mortality of adult Joshua Trees (*Yucca brevifolia*) due to small mammal herbivory at Joshua Tree National Park, California. US Geological Survey, Western Ecological Research Center, Las Vegas Field Station.
- Esque, T. C., P. A. Medica, D. F. Shryock, L. A. DeFalco, R. H. Webb, and R. B. Hunter. 2015. Direct and indirect effects of environmental variability on growth and survivorship of pre-reproductive Joshua trees, *Yucca brevifolia* Engelm. (Agavaceae). *American Journal of Botany* 102:85–91.

- Fidelibus, M., R. Franson, and D. Bainbridge. 1996. Spacing patterns in Mojave Desert trees and shrubs. United States Department of Agriculture Forest Service General Technical Report Int:182–186.
- Flores, J., and E. Jurado. 2003. Are nurse-protégé interactions more common among plants from arid environments? *Journal of Vegetation Science* 14:911–916.
- Flores-Martinez, A., E. Ezcurra, and S. Sanchez-Colon. 1994. Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana*. *Journal of Ecology* 82:325–330.
- Flores-Torres, A., and C. Montaña. 2015. From facilitative to competitive interaction between *Larrea tridentata* and *Cylindropuntia leptocaulis* in the southern Chihuahuan Desert. *Journal of Vegetation Science* 26:68–79.
- Gilliland, K. D., N. J. Huntly, and J. E. Anderson. 2006. Age and population structure of Joshua trees (*Yucca brevifolia*) in the northwestern Mojave Desert. *Western North American Naturalist* 66:202–208.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:7–26.
- Grayson, D. K. 2011. *The Great Basin: A Natural Prehistory*. University of California Press.
- Gurevitch, J., S. M. Scheiner, and G. A. Fox. 2006. *The Ecology of Plants*. Second edition. Sinauer Associates Incorporated.
- Hanley, M. E., B. B. Lamont, M. M. Fairbanks, and C. M. Rafferty. 2007. Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics* 8:157–178.
- Hansen, D. J., W. K. Ostler, and D. B. Hall. 1999. The Transition from Mojave Desert to Great Basin Desert on the Nevada Test Site. Pages 148–158 McArthur, ED, WK Ostler, and CL Wambolt, compilers. *Proceedings: Shrubland Ecotones*. Proceedings RMRS-P-11. USDA Forest Service, Rocky Mountain Research Station, Ogden, UT.
- He, Q., and M. D. Bertness. 2014. Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology* 95:1437–1443.
- Kirkham, M. B. 2014. *Principles of Soil and Plant Water Relations*. Academic Press.
- Krzywinski, M., and N. Altman. 2014. Points of significance: Visualizing samples with box plots. *Nature Methods* 11:119–120.
- Lortie, C. J., R. W. Brooker, P. Choler, Z. Kikvidze, R. Michalet, F. I. Pugnaire, and R. M. Callaway. 2004. Rethinking plant community theory. *Oikos* 107:433–438.
- Louthan, A. M., D. F. Doak, J. R. Goheen, T. M. Palmer, and R. M. Pringle. 2014. Mechanisms of plant-plant interactions: concealment from herbivores is more important than abiotic-stress mediation in an African savannah. *Proceedings of the Royal Society of London B: Biological Sciences* 281:20132647.

- Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97:199–205.
- Mahall, B. E., and R. M. Callaway. 1992. Root communication mechanisms and intracommunity distributions of two Mojave Desert shrubs. *Ecology* 73:2145–2151.
- Manning, S. J., and D. P. Groeneveld. 1989. Shrub rooting characteristics and water acquisition on xeric sites in the western Great Basin. Pages 238–244 *Symposium on Cheatgrass invasion, Shrub Die-Off and Other Aspects of Shrub Biology and Management*, Las Vegas, Nevada. April.
- Markle, M. S. 1917. Root systems of certain desert plants. *Botanical Gazette* 64:177–205.
- McAuliffe, J. R. 1984. Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. *Oecologia* 64:319–321.
- McAuliffe, J. R. 1986. Herbivore-limited establishment of a Sonoran Desert tree, *Cercidium microphyllum*. *Ecology* 67:276–280.
- McAuliffe, J. R. 1988. Markovian dynamics of simple and complex desert plant communities. *The American Naturalist* 131:459–490.
- McIntosh, R. P. 1967. The continuum concept of vegetation. *The Botanical Review* 33:130–187.
- McIntosh, R. P. 1986. *The Background of Ecology: Concept and Theory*. Cambridge University Press.
- Niering, W. A., R. H. Whittaker, and C. H. Lowe. 1963. The saguaro: a population in relation to environment. *Science* 142:15–23.
- NOAA, NCEI. 2015. National Centers for Environmental Information. <http://www.ncei.noaa.gov/>.
- O'Farrell, T. P., and L. A. Emery. 1976. *Ecology of the Nevada Test Site: A Narrative Summary and Annotated Bibliography*. Nevada Univ., Boulder City (USA). Desert Research Institute.
- Ostler, W. K., D. J. Hansen, and D. B. Hall. 1999. The Classification of Shrublands on the Nevada Test Site. Pages 12–14 *Proceedings: shrubland ecotones*.
- Padilla, F. M., and F. I. Pugnaire. 2006. The role of nurse plants in the restoration of degraded environments. *Frontiers in Ecology and the Environment* 4:196–202.
- Phillips, D. L., and J. A. MacMahon. 1981. Competition and spacing patterns in desert shrubs. *Journal of Ecology* 69:97–115.
- QGIS Development Team. 2015. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

- Ralphs, M. 2011. Broom snakeweed increase and dominance in big sagebrush communities. *Natural Resources and Environmental Issues* 17.
- Ralphs, M. H., and K. C. McDaniel. 2011. Broom snakeweed (*Gutierrezia sarothrae*): toxicology, ecology, control, and management. *Invasive Plant Science and Management* 4:125–132.
- Rasband, W. S. 1997. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA.
- Reynolds, M. B. J., L. A. DeFalco, and T. C. Esque. 2012. Short seed longevity, variable germination conditions, and infrequent establishment events provide a narrow window for *Yucca brevifolia* (Agavaceae) recruitment. *American Journal of Botany* 99:1647–1654.
- Rickard, W. H. 1965. Sodium and potassium accumulation by greasewood and hopsage leaves. *Botanical Gazette* 126:116–119.
- Rickard, W. H. 1982. Cation content of leaves of desert shrubs and its relationship to taxonomic and ecological classification. *American Midland Naturalist* 108:311–316.
- Rickard, W. H., and R. F. Keough. 1968. Soil-plant relationships of two steppe desert shrubs. *Plant and Soil* 29:205–212.
- Schwinning, S., and M. M. Hooten. 2009. Mojave Desert root systems. Pages 278–311 *The Mojave Desert: Ecosystem Processes and Sustainability*. University of Nevada Press.
- Smit, C., M. Rietkerk, and M. J. Wassen. 2009. Inclusion of biotic stress (consumer pressure) alters predictions from the stress gradient hypothesis. *Journal of Ecology* 97:1215–1219.
- Tesky, J. L. 1992. *Lycium andersonii*. <http://www.fs.fed.us/database/feis/plants/shrub/lycand/all.html>.
- Thacker, E. T., M. H. Ralphs, C. A. Call, B. Benson, and S. Green. 2008. Invasion of broom snakeweed (*Gutierrezia sarothrae*) following disturbance: evaluating change in a state-and-transition model. *Rangeland Ecology & Management* 61:263–268.
- Tirmenstein, D. A. 1999a. *Grayia spinosa*. <http://www.fs.fed.us/database/feis/plants/shrub/graspi/all.html>.
- Tirmenstein, D. A. 1999b. *Gutierrezia sarothrae*. <http://www.fs.fed.us/database/feis/plants/shrub/gutsar/all.html>.
- Tschanz, C. M., and E. H. Pampeyan. 1970. Geology and mineral deposits of Lincoln County, Nevada. Mackay School of Mines, University of Nevada.
- Turner, N. C., and P. J. Kramer, editors. 1980. *Adaptation of Plants to Water and High Temperature Stress*. John Wiley & Sons, Inc.
- Turner, R. M., S. M. Alcorn, G. Olin, and J. A. Booth. 1966. The influence of shade, soil, and water on saguaro seedling establishment. *Botanical Gazette* 127:95–102.
- USDA, NRCS. 2015. The PLANTS database. <http://plants.usda.gov>.

- Van Belle, G., L. D. Fisher, P. J. Heagerty, and T. Lumley. 2004. *Biostatistics: A Methodology for the Health Sciences*. John Wiley & Sons.
- Vandermeer, J. 1980. Saguaros and nurse trees: A new hypothesis to account for population fluctuations. *The Southwestern Naturalist* 25:357–360.
- Verwijmeren, M., M. Rietkerk, S. Bautista, A. G. Mayor, M. J. Wassen, and C. Smit. 2014. Drought and grazing combined: contrasting shifts in plant interactions at species pair and community level. *Journal of Arid Environments* 111:53–60.
- Wallace, A., and E. M. Romney. 1972. Radioecology and ecophysiology of desert plants at the Nevada Test Site. Environmental Radiation Division, Laboratory of Nuclear Medicine and Radiation Biology and Agricultural Sciences, University of California, Los Angeles. Soil Science and Agricultural Engineering, University of California, Riverside.
- Wright, A., S. A. Schnitzer, and P. B. Reich. 2014. Living close to your neighbors: the importance of both competition and facilitation in plant communities. *Ecology* 95:2213–2223.
- Yeaton, R. I. 1978. A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan Desert. *Journal of Ecology* 66:651–656.
- Yeaton, R. I., and M. L. Cody. 1976. Competition and spacing in plant communities: the northern Mohave Desert. *Journal of Ecology* 64:689–696.

## CURRICULUM VITAE

The Graduate College  
University of Nevada, Las Vegas

Eric James Chamero

### Degrees:

B.S., Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, 1999

A.S., General Studies, Manchester Community-Technical College, Manchester, CT, 1996

### Invited Presentations:

Facilitation and competition in *Yucca brevifolia* – *Grayia spinosa* nurse plant associations, Nevada Native Plant Society, Henderson, NV, March 3, 2013

Benefits to Joshua tree (*Yucca brevifolia*) resulting from relationships with larger shrubs in a desert environment, University of Nevada, Las Vegas Graduate and Professional Student Association, March 21, 2015

### Departmental Presentations:

Facilitation and competition in *Yucca brevifolia* – *Grayia spinosa* nurse plant associations, University of Nevada, Las Vegas, October 23, 2013

Facilitation and competition in *Yucca brevifolia* – *Grayia spinosa* nurse plant associations, University of Nevada, Las Vegas, March 11, 2015

### Grants and Fellowships:

University of Nevada, Las Vegas Graduate and Professional Student Association Sponsorship Fund, Fall 2014 (\$1,250)

University of Nevada, Las Vegas Graduate and Professional Student Association Sponsorship Fund, Summer 2014 (\$900)

### Thesis Title:

Assessing the importance of nurse plant associations to the growth of pre-reproductive *Yucca brevifolia*

### Thesis Examining Committee:

Committee Chair, Lawrence R. Walker, Ph.D.

Committee Member, Todd C. Esque, Ph.D.

Committee Member, Lloyd R. Stark, Ph.D.

Committee Member, Daniel B. Thompson, Ph.D.

Graduate College Representative, Stephen M. Rowland, Ph.D.