Title

From Seed Banks to Communities: Effects of Plant Invasions and Nitrogen Deposition on Desert Annual Forbs

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Publication Date

2010

UNIVERSITY OF CALIFORNIA
RIVERSIDE

From Seed Banks to Communities: Effects of Plant Invasions and Nitrogen Deposition on Desert Annual Forbs

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Plant Biology

by

Heather Elaine Schneider

December 2010

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ACKNOWLEDGEMENTS

This work was made possible by funding from the University of California Riverside Graduate Division, the University of California Riverside Department of Botany & Plant Sciences, the National Science Foundation Biocomplexity Foundation NSF (DEB 04-21530), National Park Service Air Quality/Ecological Effects Program, The Community Foundation of Riverside and San Bernardino Counties, and the Joshua Tree National Park Graduate Student Research Grant Program.

The UC Riverside Department of Botany & Plant Sciences staff, especially Rob Lennox and Douglas Holt, generously provided technical support and supplies. Much thanks to the Allen lab, past and present, for insider info, long field days, and crazy shenanigans. Special thanks go to Robert (Chip) Steers, who served as a mentor and cheerleader, and to Sara Jo Dickens, who acted as my comrade and co-conspirator. I am also grateful for Mike Bell, who never lost faith in me and was always up for an adventure. Chris True provided countless hours of help and entertainment in the field. Andrew Sanders of the UC Riverside herbarium provided invaluable plant identification assistance, as well as several forensic botany consultations for the seed bank study. This work would not have been completed without the help of Irene Ramos and Pheobe Nguyen: the best undergraduate assistants one could ever ask for.

Special thanks go to S&S Seeds for the donation of seeds and advice on germination techniques and to Landmark Plastics for donating a case of pots for the greenhouse experiment. Thank you, also, to UC Riverside Agricultural Operations, specifically Stephen Cockerham, for donating three years' worth of ammonium nitrate fertilizer.

I would like to extend my gratitude to my dissertation committee: Dr. Edith Allen, Dr. Jodie Holt, and Dr. Louis Santiago for their support, constructive criticism, and encouragement throughout this process. Special thanks go to my advisor, Dr. Edith Allen, for introducing me to the wonders of California's deserts and guiding me through five long years of graduate school. I am especially appreciative of her support for not only for my research interests, but also my passion for community service and for not only allowing but also encouraging me to think outside of the ivory tower.

Last, but not least, a heartfelt thank you goes to my incredible family and friends. First, I thank my mother and sister, whom I have missed dearly and called frequently to discuss my many successes and failures. I am eternally grateful to have people who love and support me in whatever I do. I would not be who I am today without you. Thank you, also, to my myriad of friends both near and far who provided me with endless encouragement, smiles, and laughter; you are my sanity.

DEDICATION

This work is dedicated to the memory of my father, who always believed in me and who will forever be in my heart.

ABSTRACT OF THE DISSERTATION

From Seed Banks to Communities: Effects of Exotic Plant Invasions and Nitrogen Deposition on Desert Native Annual Forbs

by

Heather Elaine Schneider

Doctor of Philosophy, Graduate Program in Plant Biology
University of California, Riverside, December 2010
Dr. Edith B. Allen, Chairperson

Desert ecosystems in California have been negatively impacted by the invasion of exotic plant species and increased nitrogen inputs due to anthropogenic nitrogen deposition. Anthropogenic nitrogen deposition acts as an artificial fertilizer in nutrient-poor desert soil, often increasing the growth of invasive species. This can alter species composition, soil nutrient cycling, and fire risk. Although several studies have focused on the impacts of increased nitrogen deposition on invasive species, fewer studies have examined its impact on native annual species and how nitrogen affects their interactions with invasive species. The purpose of this dissertation research was to understand how nitrogen deposition affects native and invasive annual species in the desert from the level of the seed to the community. A seed bank study demonstrated that, although aboveground percent cover of invasive plants can increase under nitrogen fertilization, the soil seed bank was not affected. Rather, invasive plant seeds overwhelmed the seed bank in both unfertilized and fertilized plots. A follow-up study explored seed germination responses to a range of soil nitrogen concentrations and found that species identity may be more important in determining germination differences than soil nitrogen concentration. A greenhouse study measured the growth of native and invasive annuals under a combination of nitrogen and watering treatments. This study showed that both native and invasive species could benefit from increased soil water and nitrogen availability and highlighted the importance of sufficient water in order for natives to take advantage of excess nitrogen. The invasive forb, *Erodium cicutarium*, was able to utilize increased nitrogen with less sensitivity to water availability. Finally, a field-fertilization and invasive removal study was used to elicit the effects of increased nitrogen on native annuals in the field and their competitive interactions with invasive annuals. The results demonstrated that native annuals could make use of increased nitrogen in years with sufficient precipitation and that natives can coexist with invasive species at low densities, even with high nitrogen inputs. Understanding how the annual plant community is affected by nitrogen deposition and exotic invasion is essential for the conservation and restoration of ecosystem function in California's deserts.

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General Introduction

Arid ecosystems make up 26 – 35% of Earth's land cover (Archibold 1995). When describing the deserts of California, Samuel Parish wrote, "The desert…is a land of parching heat, violent winds and scanty and irregular rainfall" (1920). Indeed, water and soil nutrients are scarce in the desert, which has lead to the evolution of a unique annual flora adapted to deal with harsh, unpredictable conditions (Mulroy and Rundel 1977, Pake and Venable 1996, Smith et al. 1997). Life in the desert exists in a delicate balance controlled primarily by the timing, distribution, and magnitude of unpredictable water pulses (Went 1948, Beatley 1967, Noy-Meir 1973). However, as the earth and how human beings use it has changed, the desert has also been altered.

For centuries, California was bombarded with introduced species from the Old World (Parish 1920, Talbot et al. 1939, Mensing and Byrne 1998, Mensing 1999, Minnich 2008), but the harsh, unaccommodating conditions of California's deserts were thought to be impenetrable to invasion. However, over time, anthropogenic effects such as urbanization, nitrogen deposition, and land-use change have degraded desert ecosystems (Parish 1920, Brown and Minnich 1986, Lovich and Bainbridge 1999, Brooks and Berry 2006) and exotic invasive annuals have become major competitors in arid lands.

Invasive species have the potential to compete with natives, reduce biodiversity, and threaten human well-being via the loss of ecosystem services such as production of food and fuel, as well as controlling water quality and quantity (Inouye et al. 1980, Brooks 2000, Díaz et al. 2006, DeFalco et al. 2007, Barrows et al. 2009). Anthropogenic nitrogen deposition can facilitate invasion in the desert by acting as an artificial fertilizer and enhancing soil nutrients, often to the detriment of native species (Brooks 2003, Allen et al. 2009, Bobbink et al. 2010). Humans have nearly doubled the input of available nitrogen to the Earth's land surface, largely through the industrial production of nitrogen fertilizer and emissions released from the burning of fossil fuels (Vitousek et al. 1997, Fenn et al. 2003b). Bobbink et al. (2010) suggest that nitrogen accumulation is the main driver of species composition changes across global ecosystem types by altering species interactions and habitat conditions. In Southern California, native ecosystems have been greatly affected by high levels of anthropogenic nitrogen deposition (Bytnerowicz and Fenn 1996, Fenn et al. 1996, Allen et al. 1997, Fenn et al. 2003a, Fenn et al. 2003b, Allen et al. 2009, Bobbink et al. 2010), as well as exotic species invasion (D'Antonio and Vitousek 1992, Minnich and Dezzani 1998, Stylinski and Allen 1999, Minnich 2008). As human land-use has expanded into the desert in the form of agriculture and urbanization, increasing levels of anthropogenic nitrogen deposition and the spread of invasive species have ensued.

In addition to inflicting detrimental competitive effects onto native species, invasive annual species also have the potential to increase fire intensity and frequency by increasing fine fuel loads in a landscape where percent cover of bare ground is typically high (Brown and Minnich 1986, Brooks 1999, Brooks et al. 2004, Rao 2008, Steers 2008). This can severely erode ecosystem health and recovery from fire in some desert communities can take decades or more (Brown and Minnich 1986, Brooks et al. 2004, Brooks and Matchett 2006, Steers 2008, Steers and Allen 2010).

Understanding the combined impacts of nitrogen deposition and exotic plant invasion on native winter annuals in the desert is imperative for creating effective conservation and restoration plans, as well as discerning how anthropogenic activities can be mitigated to protect wildlands and ecosystem services. Historically, the vegetative communities of the Colorado Desert have not been well studied (Burk 1988). In this dissertation, I attempt to understand the effects of increased nitrogen and invasive species on seeds, seedlings, and plant communities in the field, with an emphasis on the Colorado Desert.

Ephemeral annual plant species can account for up to 40% of desert vegetation, many of which exist solely as members of the soil seed bank for much of the year (Kemp 1989). Chapter 1 examines the effects of exotic plant invasion and nitrogen fertilization on soil seed bank composition and density. Field collected soil seed bank samples from unfertilized and fertilized plots were analyzed via germination in a greenhouse. Since invasive annuals have been shown to increase aboveground productivity under nitrogen fertilization (Brooks 2003, Allen et al. 2009, Rao and Allen 2010), it is important to determine how those increases translate into soil seed bank input. Seed banks are useful for understanding the history, trajectory, and restoration potential of invaded sites (Chambers 2000, Cox and Allen 2008, Gioria and Osborne 2010) and should be included in comprehensive community surveys (Major and Pyott 1966).

As a follow up to the seed bank study, Chapter 2 addresses the possible consequences of nitrogen deposition on seed germination. Several studies in both agriculture and wildland settings have demonstrated that nitrogen compounds can stimulate seed germination (Mayer and Poljakoff-Mayber 1989, Pons 1989, Dyer 1995, Plassmann et al. 2008); however, many studies have also found these effects to be species and nitrogen concentration specific (Fawcett and Slife 1978, Goudey et al. 1988, Luna and Moreno 2009). In this study, the germination of seeds from both native and invasive annual desert species was tested in a controlled environment under six levels of NH_4NO_3. Since nitrogen deposition does not affect the desert uniformly (Tonnesen et al. 2007) and has the potential to increase over time with increased urbanization and land use change, it is important to determine whether native and invasive species germination is affected differently and whether or not germination thresholds exist by which germination is either enhanced or inhibited by nitrogen. In an ecosystem where many of the native species are adapted for specialized germination and/or dormancy (Freas and Kemp 1983, Pilippi 1993), the potential effects of changes in soil nitrogen on seeds should be a topic of concern.

Assuming that native species are capable of germinating in areas subjected to nitrogen deposition, it is important to understand how increased soil nitrogen will affect physical growth. Invasive annual plants in the desert are known to acquire growth benefits from nitrogen additions (Brooks 2003, Salo 2005, James et al. 2006, Rao 2008, Allen et al. 2009, Rao and Allen 2010), but the responses of native annuals are less well understood. Furthermore, global climate change threatens to increase temperatures and make precipitation events more sporadic in the deserts of the southwestern United States (Hayhoe et al. 2004, Weiss and Overpeck 2005). In a water-limited ecosystem (Noy-Meir 1973), the combined effects of water availability and nitrogen deposition must be understood. In Chapter 3, a greenhouse experiment measured the growth responses of three native and one exotic invasive annual forb commonly found in the creosote bush scrub communities of the Colorado Desert. Low and high watering treatments were used to test for enhanced growth responses under nitrogen fertilization created by an interaction between water and nitrogen availability. Recognizing which species may perform better under high nitrogen deposition or low water availability is central for predicting the future of desert annual plant communities, as well as preparing to mitigate or prevent potentially negative effects.

Finally, in Chapter 4, a community-level approach in the field assessed the effects of nitrogen fertilization and invasive annual removal over multiple years. Annual communities are highly variable and long-term studies likely offer the best opportunity to fully understand their dynamics. However, this study offers a glimpse of how short-term fertilization and invasive removal practices, which are often more realistic in real-world scenarios, can affect community composition and productivity. This chapter also highlights the importance of invasion thresholds, which may allow native species to co-exist with invasive species at certain densities.

By measuring effects of anthropogenic nitrogen deposition and exotic species invasions in the desert at multiple small scales, one is able to paint a clearer picture of how these factors affect desert communities step by step. Furthermore, understanding the dynamics of seed banks, germination, and growth in the context of nitrogen deposition and invasion allows a more informed analysis of these problems at the community level. The information in this dissertation provides a baseline for responses of a suite of species and the potential for follow-up and expansion of these projects is immense. In the face of nitrogen deposition, exotic species invasions, and global climate change in the desert, there will likely be winners and losers. Understanding how individual species, as well as plant communities, will continue to be affected by these phenomena is imperative to conserving and/or restoring ecosystem function in the future.

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Chapter 1. Effects of elevated nitrogen and exotic plant invasion on soil seed bank composition in Joshua Tree National Park

Abstract

In this study, I investigated the effects of invasive species and nitrogen fertilization on the soil seed bank in Joshua Tree National Park, California, at four sites used in a long-term nitrogen fertilization study. In the field, invasive species responded positively to nitrogen fertilization. I compared the seed bank composition and density in control (no nitrogen added) and fertilized (30 kg N $ha^{-1}yr^{-1}$) plots to determine if the seed bank would reflect aboveground changes due to nitrogen fertilization. Soil samples were collected and germinated in a greenhouse over two years. 1,632 seedlings representing 27 species from 14 families germinated throughout the course of the study. The hypothesis that seed bank composition and density would reflect the previously measured aboveground plant community changes that occurred under nitrogen fertilization was not supported. While no significant differences were detected between treatments within sites, exotic invasive grass seeds overwhelmed the seed bank at all sites. Significant differences among sites were found, which may be due to differences in level of invasion, historic nitrogen deposition, and soil texture. Sites experiencing low nitrogen deposition had the highest species richness for both control and fertilized treatments. Aboveground plant density did not correlate well with seed bank density, which is typically due to the inherent

patchiness of soil seed banks. Soil seed bank studies can provide valuable insight into the history of a site, as well as magnitude of invasion and restoration potential at invaded sites.

Introduction

A soil seed bank is a collection of viable seeds in the soil that have not yet germinated (Roberts 1981). Many species use soil seed banks as a bet-hedging strategy in stochastic environments (Cohen 1966, Pake and Venable 1995, Guo et al. 1999). Soil seed banks help to ensure species persistence and maintain genetic diversity (Templeton and Levin 1979). The composition of the soil seed bank is influenced by aboveground species composition, seed output, and longevity of individual seeds (Coffin and Lauenroth 1989, van der Valk and Pederson 1989, Benvenuti 2007), as well as soil texture, recent environmental cues, and disturbance history (Coffin and Lauenroth 1989, Benvenuti 2007). Soil texture, in particular, can affect seed burial and emergence from the seed bank with coarse-textured soils generally burying seeds more easily than fine-textured high-clay soils (Hopkins and Graham 1983, Benvenuti 2003, 2007). Seed banks can also offer a glimpse into the history of species composition at a site and reflect its future trajectory and restoration potential.

Seed banks are commonly used by native annual forbs in harsh, unpredictable environments. Deserts are subject to extreme temperatures and highly variable rainfall, creating a favorable scenario for the use of soil seed banks. The formation of soil seed banks is closely related to life history and seed size, with annual small-seeded species being more likely to form seed banks than large-seeded or perennial species (Honda 2008). Annual species strongly relying on seed banks can account for up to 40% of desert vegetation and, in periods of drought, species may exist solely as seeds in the soil seed bank rather than as part of the aboveground community (Kemp 1989). Desert annual species are often equipped with specialized germination requirements and/or innate dormancy that allows them to avoid unfavorable conditions (Freas and Kemp 1983, Pilippi 1993) while holding their place in space belowground, although dormancy is not a requirement for forming a persistent seed bank (Thompson et al. 2003, Honda 2008).

Seeds stored in soil seed banks can fall victim to a number of fates including successful germination, mortality, predation, or failed germination. One threat to native soil seed banks that may be overlooked is exotic plant invasion. Invasive species are widely recognized as having detrimental effects on aboveground plant communities (Elton 1958, Brooks 2000b, Mack et al. 2000, Cione et al. 2002), but they can also negatively impact the belowground plant community by altering soil the seed bank (Vila and Gimeno 2007, Cox and Allen 2008, Gioria and Osborne 2009b, Gioria and Osborne 2010). Exotic invasive species often produce high numbers of readily germinable seeds and may not be well adapted to using long-term seed banks (Baker 1974, Wu and Jain 1979). The exotic invasive annual grass *Bromus madritensis* ssp. *rubens*, for example, has 100% seed viability at maturity (Wu and Jain 1979) and exhibits maximum dormancy of two to three years (Brooks 2000a). For this reason, it has been suggested that populations of exotic invasive grasses cycle between flourishing and crashing with variation in precipitation (Salo 2004). However, seeds of invasive plants can overwhelm the soil seed bank in the short term (Cox and Allen 2008). For example, *Schismus arabicus*, an invasive annual grass commonly found in deserts and semi-arid areas of Southern California, produces copious amounts of seed but only part of the seed bank germinates each year, leaving the rest for future growing seasons (Gutterman 1994). Furthermore, the seeds of *Erodium cicutarium*, an invasive annual forb that is found throughout the USA is native to the Mediterranean region, may survive in the soil for over 35 years (Hull 1973), which could confer a competitive advantage in the presence of multi-decadal droughts. It is unclear how long native annual forbs can remain viable in desert soils (Thompson et al. 1993, Bekker et al. 1998, Moriuchi et al. 2000), but it is commonly assumed that they are adapted for extended storage periods.

Seed banks represent an important portion of plant populations that exist belowground, may not be apparent aboveground for many years, and may be overlooked during invasive species impact assessments and restoration efforts (Cox and Allen 2008). When exotic invasive species heavily invade an area, they can overwhelm the soil seed bank. This becomes problematic because it creates a new dimension of competition belowground. Invasive species often produce higher numbers of seeds, have an earlier and more rapid phenology, and use resources more quickly than native species (Baker 1974, Brooks 2000c). When the soil seed bank is compromised by invasive species, it can create a positive feedback cycle for invasives by increasing their density both above and belowground. Additionally, it decreases the potential for passive restoration of an invaded site and complicates active restoration efforts by requiring seed bank management in addition to aboveground invasive weed control.

In addition to exotic invasive species, nitrogen deposition also threatens California's desert ecosystems. Joshua Tree National Park (JTNP) is affected by anthropogenic nitrogen deposition from the Los Angeles air basin (Fenn et al. 2003b, Allen E.B. et al. 2009, Allen 2009, Rao et al. 2009, Rao and Allen 2010). Nitrogen deposition from the combustion of fossil fuels and agricultural fertilizers is altering soil nutrient levels and fertilizing desert soils (Fenn et al. 2003a, Allen EB et al. 2009, Allen et al. 2009). The desert is particularly sensitive to increased soil nitrogen levels and, in some areas, invasive annual grasses and forbs now dominate where natives once flourished (Brooks 2000b). Changes in aboveground vegetation due to elevated nitrogen may translate into seed bank composition changes (Kitajima and Tilman 1996). Furthermore, increased soil nitrogen from deposition may affect germination from the seed bank, thereby altering the aboveground community that replenishes it (Plassmann et al. 2008). Historically, California's deserts have been less developed than the large coastal urban areas to the west. However, as urbanization continues to spread eastward, anthropogenic pollution and land disturbance increasingly threaten native desert ecosystems.

In this study, I investigated the effects of nitrogen fertilization and exotic plant invasion on the soil seed bank in the deserts of Southern California. The primary goal of this study was to determine whether the soil seed bank reflected aboveground community changes associated with increased nitrogen that were observed as part of a nitrogen fertilization study conducted in Joshua Tree National Park (Allen et al. 2009). Specifically, I wanted to explore the possible seed bank density and composition differences between unfertilized plots and plots that had been fertilized for three years with ammonium nitrate. It is important to understand how aboveground vegetation changes relate to seed bank changes in an invaded community because aboveground plants consistently contribute to the seed bank by depositing seeds onto the soil. Seed bank species composition and abundance have direct impacts on conservation and restoration potential for invaded sites.

Methods

Study site

This research took place at Joshua Tree National Park (JTNP). Located in Southern California, the 320,000 ha park encompasses portions of both the low elevation Colorado and high elevation Mojave deserts. Over 700 plant species have been identified within JTNP, including some federally listed species. The Park is part of a west-to-east nitrogen deposition gradient, with deposition being highest at the western edge of the Park and lower near the middle and eastern portions (Allen et al. 2009, Rao et al. 2009).

Four sites that were part of another study examining the effects of nitrogen fertilization on native and invasive annual species were used for this research (Brooks 1999, Allen 2009). The sites were paired low and high nitrogen deposition sites in the low elevation Colorado Desert and high elevation Mojave Desert in JTNP. The two low elevation sites are located in Pinto Basin and Wide Canyon. Pinto Basin is designated as Creosote Bush Low Deposition (CB Low; 33°49’53.724”, 115°45’30.247”; elev. 750m) and Wide Canyon is designated as Creosote Bush High Deposition (CB High; 33°56’45.882”, 116°23’41.116”; elev. 550m). Both sites are dominated by creosote bush scrub (CB) vegetation, with *Larrea tridentata* (creosote bush) as the most common perennial shrub. Pinyon-juniper (PJ) woodland (*Pinus monophylla* and *Juniperus californica*) dominates the high elevation sites located at Pine City and Covington Flat. In this paper, Pine City will be referred to as Pinyon-Juniper Low Deposition (PJ Low; 34°2’14.554”, 116°4’28.159”; elev. 1400m) and Covington Flat will be called Pinyon-Juniper High Deposition (PJ High; 34°0’50.184”, 116°18’48.841”; elev. 1500m). Nitrogen deposition at each site was estimated using a deposition model (Tonnesen et al. 2007). Nitrogen deposition was measured to be 3.4 kg N ha^{-1}yr^{-1} at CB Low and 5.2 kg N ha^{-1}yr^{-1} at CB High. PJ Low receives approximately 6.2 kg N ha^{-1}yr $^{-1}$ in deposition, while PJ High receives 12.4 kg N ha^{-1}yr^{-1} (Allen et al. 2009, Rao et al. 2009). Soil texture is sandy loam at all sites with a variable amount of gravel and rocks (Allen et al. 2009, Rao et al. 2009). CB Low is part of a basin that accumulates sand and represents the least rocky site. CB High is a gravelly debris flow; PJ Low, which is the rockiest site, is a rocky alluvial channel; and PJ High is an alluvial fan (Allen et al. 2009).

Fertilization experiment

Field plots were set up in a randomized block design at four sites: CB Low, CB High, PJ Low, and PJ High. Plot size was dependent on shrub or tree size at each site. In the low elevation Colorado Desert, each plot was centered on an individual creosote bush (*L. tridentata*) and measured 6 x 6m. High elevation Mojave Desert plots were 8x8m and centered on juniper shrubs (*J. californica*). Each site consisted of 10 replicate blocks containing each treatment with the exception of PJ Low, which only had 9 blocks. Three nitrogen fertilization treatments (0, 5, and 30 kg N ha^{-1}) were applied to field plots every December from 2002 – 2005 using granular ammonium nitrate (NH_4NO_3) (Allen et al. 2009). This seed bank study utilized control (0N added) and high-fertilized (30kg N ha^{-1}) only. Although fertilization of the high nitrogen plots ceased after 2005, the vegetation was sampled through 2010.

Five-centimeter deep soil cores were collected to monitor extractable soil nitrogen (see Allen et al. 2009 for details on soil sampling). Soils were extracted using a KCl solution and extractable nitrogen (NH_4^+ and NO_3^-) was measured using a flow-injection analyzer at the University of California Division of Agriculture and Natural Resources Laboratory (danranlab.ucdavis.edu; Table 1). Vegetation was monitored in 1.0 x 0.5m quadrats beyond the shrub drip line on the north and south sides of shrubs, for a total of two quadrats per shrub. Percent cover was measured within plot frames and species richness was recorded for the entire plot in April or May each year (Allen et al. 2009).

Community composition data were not collected during the years prior to and after seed bank analysis because drought reduced annual plant germination, so both aboveground plant density and cover data were collected in 2009 and 2010 to generate regressions to estimate density values in other years. These plant density values were used to compare with seed bank densities.

Seed bank sampling

In the fall of 2006, soil seed bank samples were collected from every block at each site. Only control (no nitrogen added) and high-fertilized (30 kg N $ha^{-1}yr^{-1}$) plots were used for seed bank sampling. A 9cm diameter x 5cm deep soil corer was used to collect samples from the north and south side of each shrub. Four samples were collected and combined to create a composite sample representing either the north or south side of the shrub, resulting in two composite samples per shrub and 156 samples total from all four sites. Soil samples were collected from just beyond the shrub drip line (Figure 1) to coincide, but not interfere, with vegetation measurements from the field fertilization study.

Seed bank germination

Soils were transported to the University of California, Riverside, air dried, and stored at 7ºC prior to germination. Seed bank composition was determined via germination (Roberts 1981, Gross 1990, Cox and Allen 2008). A 400mL subsample of soil from each composite sample was sieved through a 5mm mesh to remove large rocks and debris and mixed with equal parts sand to provide adequate substrate for germination and growth. The soil was placed in 20x20cm Styrofoam trays in a greenhouse and labeled according to site, block, direction, and treatment (control or fertilized). The depth of the soil mixture in each tray was approximately two centimeters. The trays were watered liberally with deionized water to stimulate germination. Seedlings were marked, identified, and recorded as they appeared until germination ceased. Unidentifiable seedlings were transplanted into pots filled with UC Soil Mix III, which is predominantly made up of plaster sand and peat moss, and allowed to grow until identification was complete, generally in two to three weeks and occasionally until flowering occurred. When germination ceased, the soils were allowed to dry, were stirred, and then watering was resumed. During the final germination cycle, a 4% gibberellic acid solution was added to the soils to induce germination. The experiment was concluded after three rounds of germination through multiple seasons. The first round of germination lasted for 4 months from February through May of 2007. The second round of germination was the longest and lasted from October 2007 through March of 2008. The final round of germination lasted only one month in February of 2009. Two summer watering treatments, one in 2007 and one in 2008, were attempted but did not result in any germination.

Data analysis

Seed bank density was calculated as seeds/m^2 from seedlings/tray. Species were grouped into functional groups as invasive grass, invasive forb, and native forb for analysis. Since only one native grass seedling emerged, it was included in the native forb category. Data were analyzed by treatment to compare fertilized (30kg N ha^{-1}) and control (0N added) plots. Seed bank density and richness data were extremely non-normal and resisted transformation; therefore, analyses were performed using the Kruskal-Wallis Test for non-parametric data. Non-normal data are common for seed bank studies due to the high number of zero values commonly encountered and the data are often resistant to transformation (King and Buckney 2001, Gioria and Osborne 2009a). Post-hoc tests were done using Tukey's Honestly Significant Difference with $\alpha = 0.05$. All data were analyzed using JMP® statistical software (JMP, Version 8). Sørensen's Similarity Index was calculated to determine similarity between treatments within sites and similarity between treatments among sites. Sørensen's Similarity Index is calculated as IS = [2C/(A+B)] x 100, where C is the number of species each sample (or site) has in common and A and B represent the number of species found in each sample.

Aboveground plant density data from 2009 and 2010 were used to create a regression between percent cover and density. Data from both years were analyzed together to improve the regressions and there were no significant differences between years. Plant density data were transformed (log + 0.5) to linearize the data. These regressions were used to estimate density in the seasons before and after seed bank analysis. Due to the low occurrence of invasive forbs, invasive forb and grass densities were added together and analyzed as total invasive density. Aboveground percent cover data from 2006 were used to compare seed bank density with the "seed bank donor population" from the season prior to seed bank sampling. Due to low rainfall (Table 2), no vegetative data were recorded at CB Low in 2006, so 2005 data were used for that site. Extreme drought in 2007 again prevented germination at the four sites, so vegetative data from 2008 were used to compare seed bank density with the aboveground community that emerged following soil seed bank collection. Linear regression was used to relate seed bank density with calculated aboveground plant density. Nomenclature follows Hickman (1996).

Results

Over the course of this experiment, 1,632 seedlings from 27 species in 14 families emerged from the soil seed bank. Thirty-three seedlings were unidentifiable due do premature death. Five of the identified were exotic invasive species and 22 were native (Table 3). CB Low had the highest number of seeds germinate, while PJ Low had the lowest.

There were no significant differences between the north and south sides of shrubs (Table 4), therefore, data from north and south sides were combined for statistical analysis. Few differences were found between control and fertilized plots within sites (Table 5) with the exception of CB High, which showed higher native seed density in control versus fertilized plots (H = 4.8, 1df, p = 0.0284). Despite the lack of a nitrogen effect within sites, differences were detected among sites (Table 6). PJ Low had higher native seed density in the control treatment than any other site (H = 15.62, 3df, p = 0.0014), as well as the highest native seed density in fertilized plots, although it was not different from CB Low (H = 22.33, 3df, $p < 0.0001$) (Figure 2a; Table 3). Invasive density was lower at PJ Low than other sites in control and fertilized plots (H = 18.74, 3df, p = 0.0003, H = 18.37, 3df, p = 0.0004 respectively) and CB Low consistently had the numerically highest density of invasive plants, mostly invasive grasses (Figure 2b; Table 3).

Although species richness did not differ by treatment within sites, between site differences did exist. PJ Low and CB Low had the highest species richness in both control (H = 17.65, 3df, p = 0.0005) and high-fertilized (H = 19.48, 3df, p = 0.0002) plots (Figure 3), although average species richness was low at all sites.

Sørensen's Similarity Index was used to compare species composition between treatments. Low Sørensen's values represent low species similarities and values close to 100 are extremely similar. Similarity was low between control and fertilized plots within sites (Table 7). Between-site similarity was calculated for control and fertilized plots and values were low for all combinations, although CB Low and CB High were more similar than PJ Low and PJ High (Table 7). The highest similarity between treatments within a site was found at CB High with 54.5% similarity.

Exotic invasive seedling emergence decreased over successive germination periods; however, seeds of *Schismus* species continued to germinate in low numbers throughout the duration of the study. Native winter annual forbs germinated throughout the study. The first summer watering treatment failed to stimulate germination of either invasive or native species. One summer annual grass, *Bouteloua aristidoides*, germinated during the second summer watering treatment and was the only summer annual to germinate in the course of the study.

Aboveground plant density in the year preceding sampling was not a good predictor of seed bank density, nor was seed bank density a good predictor of aboveground plant density the season following seed bank collection (Table 8). For native forbs, only two of the 16 regressions were significant. For invasives, five out of the 16 regressions were significant. The sites used in this study are not productive enough to elicit a strong self-thinning effect; therefore, the relationship is unlikely to be non-linear. The strongest relationship between seed bank and aboveground density was represented by invasive density in PJ Low control plots in 2006 ($R^2 = 0.40$). R-square values ranged from 0.00003 to 0.40. Three regressions yielded R-square values very close to zero and only seven out of 32 regressions had slopes that were significantly different from zero, indicating few relationships between seed bank density and annual plant density.

At three of the sites, one or more species emerged from the seed bank that had not been previously identified as part of the aboveground community since the fertilization experiment began in 2003. Three novel species emerged from PJ Low soils. The exotic invasive forb *Erodium brachycarpum* and the native annuals *Euphorbia setiloba* and *Portulaca halimoides* had not previously been observed at this location. *Chaenactis stevioides*, a native annual forb, had not been recorded at CB Low or CB

High during aboveground surveys and *Chamaesyce albomarginata* did not appear on the species list for CB Low. These species demonstrate the archival nature of soil seed banks.

Discussion

Nitrogen and soil texture impacts on seed banks

My hypothesis that the seed bank would reflect aboveground plant community changes that occurred under nitrogen fertilization was not supported. No significant differences in species richness or seed density were detected within sites under different nitrogen treatments. However, seed bank differences between sites were detected. This may be evidence that short-term nitrogen inputs are not enough to alter desert seed bank dynamics, but long-term differences due to site-specific characteristics such as soil texture and long-term nitrogen deposition can influence species dynamics. Increased nitrogen at sites with finely textured soils, such as PJ High and CB Low, may create a more hospitable environment for invasive species to establish as compared to low nitrogen, rocky sites such as PJ Low. In general, sandy soils offer a more hospitable environment for soil-stored seed banks as compared to very fine-textured soils, such as clay, by allowing for easier, deeper burial (Hopkins and Graham 1983, Benvenuti 2003, 2007). At these sites, the soils were all sandy loam, but possessed a different amount of rock and gravel. We propose that a higher percentage of rock and gravel impedes seed burial and subsequent germination, especially for exotic invasive species, which tend to have larger seeds than native desert annuals (Schneider Chapter 2.).

Research on the effects of elevated soil nitrogen on seed bank density and composition is lacking in the literature. One study suggested that elevated nitrogen from atmospheric deposition could alter soil seed banks in coastal slack dunes (Plassmann et al. 2008). However this was inferred from enhanced germination of seeds from the seed bank following fertilization in a greenhouse. In my study, I wanted to discern whether or not multiple years of nitrogen fertilization in the field altered seed bank composition and density when compared to unfertilized plots. No nitrogen was added in the greenhouse.

Nitrogen deposition has the potential to affect soil seed bank composition because of its effects on aboveground vegetation and seed germination. Elevated soil nitrogen can enhance biomass production of plants in the desert (Brooks 2003, Allen et al. 2009, Rao and Allen 2010), which could lead to increased seed production because biomass and fecundity may be positively correlated (Cousens and Mortimer 1995). Studies have shown that elevated nitrogen can increase seed production (Zhao et al. 1993, Baldwin et al. 1998) and nitrogenous compounds are well-known germination stimulants (Hendricks and Taylorson 1974, Plassmann et al. 2008, Sweeney et al. 2008), which could affect inputs into and germination out of the soil seed bank.

In this study, the seed bank does not reflect the relatively small increase in percent cover of invasive grass due to nitrogen fertilization over three years; however, it does reflect differences between sites. The only site that showed significant differences in seed bank density was CB High, which had higher native seed density in control versus fertilized plots. This effect is likely the result of an increase in invasive cover in fertilized plots in 2005 (Table 9), which led to low native cover and, in turn, low native seed production. Although nitrogen deposition varied between sites, initial extractable soil nitrogen did not differ. Fertilization increased soil nitrogen compared to control treatments at all sites across all years of the study. These differences may be due, in part, to historic invasion levels, as well as soil texture differences. Soil rockiness has been suggested to influence invasion dynamics, with rocky sites being less invaded (Rao et al 2009). The high level of exotic grass invasion at the lowest deposition site, CB Low, which also has the fewest rocks, demonstrates this. The magnitude of invasion at CB Low is comparable to that of CB High, which is its paired high nitrogen deposition site. This relationship differs from the relationship between PJ Low and PJ High, where the low deposition site, PJ Low, is much less invaded than its high nitrogen deposition paired site, PJ High. It appears that, in this case, soil texture could be more important than the amount of nitrogen being deposited at the site. In the field fertilization study, the rockiest site, PJ Low, showed no change in invasive grass cover with nitrogen fertilization, but native forbs did increase (Allen et al. 2009). PJ Low also had higher native forb seed density than any other site. The relationship between invasion and soil texture should be further investigated to determine its influence on seed bank dynamics.

The seed bank also demonstrates that less invaded areas tend to have a higher density native seed bank, whereas highly invaded sites reflected the invasion in the seed bank as well as aboveground vegetation. This was evidenced by the consistently high density of native seeds at PJ Low, which was also the least invaded site. Furthermore, Sørensen's Similarity Index hovered between 40 – 50% for control and fertilized plots within the same site. These differences in species composition suggest that although nitrogen fertilization did not affect seed density by functional group, species composition can be altered due to nitrogen fertilization. Taken together, the results of this study imply that exotic invasions can influence seed bank dynamics, although it remains uncertain to what extent this is occurring. Previous studies have shown that highly invaded areas and lands subjected to post-invasion type conversion can suffer extreme degradation of the soil seed bank (Cox and Allen 2008, Gioria and Osborne 2010). If conditions continue to favor the success of exotic invaders, this could pose a serious threat to the native plant communities in Joshua Tree National Park.

Considerations for soil seed bank studies

There has been much discussion over methods for quantifying seeds stored in the soil seed bank (Roberts 1981, Bigwood & Inouye 1988, Gross 1990, (Ter Heerdt et al. 1996, Caballero et al. 2008). One limitation of germination assays in seed bank studies is that each species has different requirements for germination. The greenhouse environment can vary from field conditions in terms of temperature, light, humidity, and other natural processes such as wind and animal disturbance. Seeds adapted to using a soil seed bank remain in the soil until successful germination and establishment can be achieved or until seed death. Germination in the field is variable between years and it is difficult to meet the requirements of each species at one time under artificial conditions.

Another limitation of seed bank studies is that soil seed bank sampling is affected by extreme spatial and temporal variation of seed distribution in the soil (Reichman 1984). Many desert plant species are adapted to having relatively short dispersal distances (Ellner and Shmida 1981), which can lead to localized seed patches. Furthermore, seed distribution can be affected by both biotic and abiotic factors such as seed size and shape, granivory, and animal dispersal (Chambers and MacMahon 1994). Habitat type, soil microtopography, variation in persistence of species, precipitation, and seasonality can also affect seed distribution (Thompson and Grime 1979). These factors create many challenges for accurately sampling the soil seed bank. The results of a seed bank study will be influenced by the patchy distribution of seeds in the field, which microsites are chosen for sampling, the size and shape of soil cores, and the seed enumeration method used. This patchy seed distribution also causes some soil seed bank samples to contain few or no seeds (Busso and Bonvissuto 2009). For these reasons, it is uncommon for seed bank densities to be strongly correlated with measured aboveground field densities (Thompson 1986, King and Buckney 2001, Vila and Gimeno 2007).

For this study, I used a composite sampling method in an effort to homogenize patchy seed distribution, but still found very weak relationships between above and belowground species composition and density. The lack of correlation between the seed bank and the donor population from 2005 indicates the complexity of seed bank dynamics, which encompasses long-term processes, stochastic events, and large variation between years. The 2006 season, when seed bank samples were collected, was a slightly below average precipitation year. Aboveground plant density was measured in 2009, another below average precipitation year, and in 2010, which was an average year. Density calculations for 2006 were based on regressions using data from both years. Annual variation in precipitation would vary the relationship between seed density and cover, but not change the heterogeneous relationship of soil microsite with seed density and seedling establishment. Despite the many difficulties associated with examining soil seed banks, germination studies can be useful for revealing readily germinating species existing as seeds in the soil. In the case of JTNP, it appears that the seeds of exotic invasive species overwhelm the soil seed bank in both control and high-fertilized plots at all sites.

Another benefit of using germination assays to determine seed bank composition and density is that it can elucidate important information about timing of germination under favorable conditions. In this study, the invasive grasses *Schismus* spp. and *B. madritensis* ssp. *rubens* germinated earlier than any other species in the seed bank, which is in keeping with Baker's early and rapid phenology characteristics of an ideal weed (Baker 1974). Seeds of both species appeared to be readily germinable and were present in large numbers. *B. madritensis* ssp. *rubens* only occurs at the high elevation sites due to a higher demand for water than *Schismus*, which is found at all sites but is most abundant at the drier, low elevation sites (Brooks 2000 a, c, Salo 2004). Since native annual forbs in the desert ecosystem are adapted to long-lived seed banks and conservative germination (Kemp 1989, Pake and Venable 1996, Venable 2007), it is likely that native seeds remain un-germinated in the soil samples I collected. Additional treatments to induce germination could generate more information about the number and identity of seeds in the soil.

Implications for monitoring and restoration

The soil seed bank can provide important information about population and community level dynamics, both of which can be useful to plant ecologists, land managers, and restoration ecologists (Chambers 2000, D'Antonio and Meyerson 2002, Gioria and Osborne 2010). Seed bank studies can be strongly influenced by the method and timing of collection, as well as how the number of seeds in the soil is enumerated (Roberts 1981). For this reason, it is important for the goals of a seed bank study to be determined prior to collection of samples. In this study, a nitrogen treatment was included to understand how increased nitrogen deposition might influence exotic invasion and seed bank dynamics.

Information about long-term invasion effects and both passive and active restoration potential at a site can be elucidated from seed bank studies, and the resiliency of a site to disturbance will rely, in part, on the state of its soil seed bank (van der Valk and Pederson 1989, D'Antonio and Meyerson 2002, Luzuriaga et al. 2005). The ability of some invasive species to contaminate the soil seed bank highlights the need for invasive species management to be implemented on both the above and belowground community. If management of the soil seed bank is not possible, it is important for aboveground removal projects to be timed appropriately to prevent invasive plant seed deposition into the seed bank. In this study, I found that exotic seeds overwhelmed the seed banks at three of the sites, suggesting that passive restoration of these sites would be impractical.

This study attempted to elicit the combined effects of nitrogen deposition and invasive species on an annual plant community that relies heavily on a soil seed bank. Aboveground shifts in invasive plant percent cover due to nitrogen fertilization (Allen et al. 2009) led me to investigate whether soil seed bank composition and density were also changing. The results suggest that between-site differences such as soil texture may also be important factors affecting seed banks, however exotic invasive seed still overwhelmed the soil seed bank at all sites. The degree to which the soil seed bank has been degraded in sites experiencing invasion suggest that the native plant community is at risk of being compromised and seed bank management may be necessary for successful conservation and restoration. Studying plant communities at multiple spatial and temporal scales strengthens conservation efforts by producing a more accurate description of species composition and density at a site. As urbanization continues to expand eastward into the desert in Southern California, it is likely that nitrogen deposition will continue to increase. Fertilization studies can offer us a glimpse of how increased nitrogen deposition may affect certain areas in JTNP in the future. Continuing to refine soil seed bank techniques will also help to create a more complete picture of the effects of exotic invasions and to understand the long-term implications of invasion at multiple scales.

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Table 1.1. Soil nitrogen concentrations [µg/g extractable NH_4^+ plus NO_3^- (S.E.)] in response to fertilizer treatments (control and 30 kg N/ha) in the years before, during, and after seed collection and prior to plant density determinations. Fertilization ceased prior to the 2006 soil collection. Significant differences are denoted by an asterisk (*).

	Extractable Soil Nitrogen (NH_4^+, NO_3^-)							
Site	**2005**		**2006**		**2007**		**2008**	
	Control	**Fertilized**	**Control**	**Fertilized**	**Control**	**Fertilized**	**Control**	**Fertilized**
CB Low	3.6 (0.16)	13.76 (2.5)*	5.49 (0.48)	7.53 (1)	7.7 (0.58)	10.51 (0.81)	7.17 (0.51)	8.48 (0.78)
CB High	4.34 (0.44)	10.02 (1.92)*	5.92 (0.65)	10.08 (2.72)	9.7 (1.7)	15.22 (2.55)	7.49 (0.72)	9.63 (1.64)
PJ Low	3.45 (0.14)	10.39 (2.15)*	10.51 (2.66)	14.15 (2.29)	7.26 (0.58)	9.55 (1.48)	7.75 (0.61)	11.79 (1.28)
PJ High	3.89 (0.28)	16.85 (3.48)*	5.64 (0.39)	12.99 (2.32)*	9.01 (1.09)	12.13 (1.42)	7.68 (0.4)	11.67 (1.64)

Figure 1.1. Seed bank sampling design. Four samples were collected around a $0.5m^2$ plot frame from the north and south sides of shrubs using a 9cm diameter soil corer to a depth of 5cm. Samples were composited into one north side and one south side sample per shrub. Samples were collected from shrubs in control (unfertilized) and fertilized (30kgN/ha) plots at each site. Plots were centered on a creosote bush (*Larrea tridentata*) at the low elevation sites (Pinto Basin and Wide Canyon) or a juniper (*Juniperus californica*) at the high elevation sites (Pine City and Covington Flat).

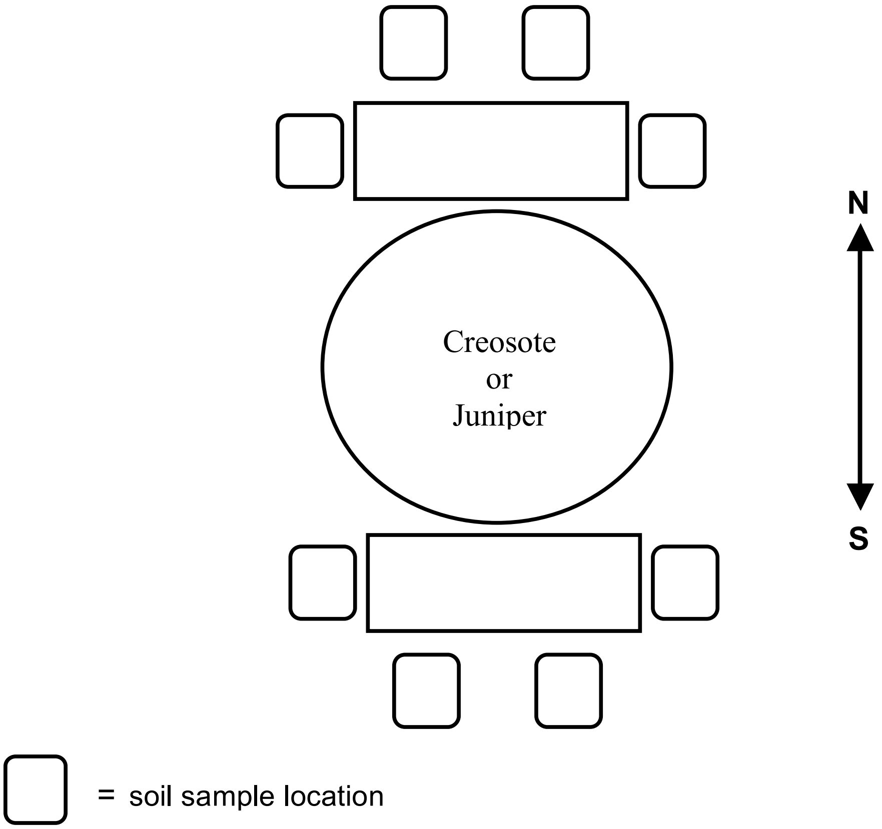

Table 1.2. Winter growing season precipitation for 2005 – 2010 at all sites. Precipitation is measured in centimeters (mm).

	Winter Precipitation (mm)			
Growing Season	**PJ Low**	**PJ High**	**CB Low**	**CB High**
Jan - April 2005	108.7	178.3	89.2	205.5
2005 - 2006	53.3	108.5	22.9	60
2006 - 2007	20.8	24.3	21.3	7.4
2007 - 2008	100.8	149.6	59.9	102.1
2008 - 2009	51.3	73.6	N/A	N/A
2009 - 2010	175.2	214	149.8	177.8

Table 1.3. Numbers of germinants/m^2 for each species from soils collected in Joshua Tree National Park from four sites: CB = creosote bush, PJ = pinyon-juniper, Low = low N deposition site, and High = high N deposition site. *Schismus arabicus* and *S. barbatus* could not be differentiated as seedlings but both species exist at these sites.

Functional Group	Family	Species	CBS Low	CBS High	PJ Low	PJ High
Exotic Grass	Poaceae	*Bromus rubens*	0	0	32	394
		Schismus arabicus & *Schismus barbatus*	531	366	73	16
Exotic Forb	Brassicaceae	*Brassica tournefortii*	0	6	0	0
	Geraniaceae	*Erodium brachycarpum*	0	0	3	0
		Erodium cicutarium	1	0	19	0
Native Forb	Asteraceae	*Chaenactis stevioides*	2	2	1	2
		Filago depressa	0	1	3	0
	Boraginaceae	*Amsinckia tessellata*	1	0	4	0
		Cryptantha angustifolia	12	6	2	0
		Cryptantha spp.	0	0	1	0
		Pectocarya heterocarpa	5	1	0	0
	Brassicaceae	*Descurainia pinnata*	0	0	10	0
		Lepidium lasiocarpum	0	0	1	0
	Crassulaceae	*Crassula connata*	0	1	0	0
	Euphorbiaceae	*Chamaesyce albomarginata*	0	1	51	0
		Chamaesyce setiloba	0	0	1	0
	Fabaceae	*Lotus strigosus*	7	0	3	0
	Hydrophyllaceae	*Phacelia fremontii*	0	0	2	0
		Phacelia spp.	0	0	2	0
	Lamiaceae	*Salvia columbariae*	0	0	0	3
	Molluginaceae	*Mollugo* spp.	0	0	7	1
	Onagraceae	*Camissonia claviformis*	2	0	0	0
	Poaceae	*Bouteloua aristidoides*	0	0	1	0
	Polemoniaceae	*Gilia* spp.	0	0	1	0
	Portulacaceae	*Calyptridium monandrum*	0	0	0	1
		Portulaca halimoides	0	0	7	0
	Unknown	Unknown	22	1	7	3
Total			583	385	231	420

Table 1.4. Analysis of total seed density from north versus south sides of shrubs by site showed no differences due to aspect. Significant differences were determined using a Kruskal-Wallis test ($p < 0.05$; 1df).

Site	H-value	p-value
PJ Low	2.55	0.1101
PJ High	0.061	0.8054
CB Low	0.036	0.8495
CB High	2.1	0.1473

Table 1.5. Analysis of total seed density between control and fertilized plots by site showed no differences due to nitrogen treatment using a Kruskal-Wallis test ($p < 0.05$; 1df).

Site	H-value	p-value
PJ Low	1.11	0.2917
PJ High	1.082	0.2983
CB Low	0.036	0.8495
CB High	0.01	0.92

Table 1.6. Seed density [germinants/m^2 (S.E.)] by site and control vs. nitrogen treatment. Significant differences are shown with superscripts across rows. Values that do not share similar letters are significantly different ($\alpha = 0.05$). Values with no superscript letters or symbols are not different. CB = creosote bush, PJ = pinyon-juniper, Low = low N deposition site, and High = high N deposition site.

	Seeds/m^2				
Functional group, treatment	**CB Low**	**CB High**	**PJ Low**	**PJ High**	**P-value**
Native Control	**137.5^{B} (31.3)**	**56.3^{B} (19.2)**	**381.9^{A} (119.8)**	**37.5^{B} (18.4)**	**0.0014**
Invasive Forb Control	**0^{B} (0)**	**37.5^{AB} (37.5)**	**118.1^{A} (49.0)**	**0^{B} (0)**	**0.0008**
Invasive Grass Control	**1593.8 (292.3)**	**1037.5 (683.6)**	**479.2 (172.8)**	**1212.5 (494.7)**	**0.0003**
Native Fertilized	**181.3^{AB} (54.8)**	**25.0^{B} (25.0)**	**340.3^{A} (108.8)**	**25.0^{B} (11.5)**	**< 0.0001**
Invasive Forb Fertilized	**6.25 (6.25)**	**0 (0)**	**34.7 (28.2)**	**0 (0)**	**0.2379**
Invasive Grass Fertilized	**1725.0^{A} (338.4)**	**1250.0^{AB} (538.3)**	**250.0^{B} (126.6)**	**1350.0^{AB} (322.5)**	**0.0004**

Figure 1.2. Average seed bank species richness under control and fertilized treatments. Average seed bank richness was calculated per tray at the end of the study. Values separated by different letters are significantly different ($\alpha = 0.05$).

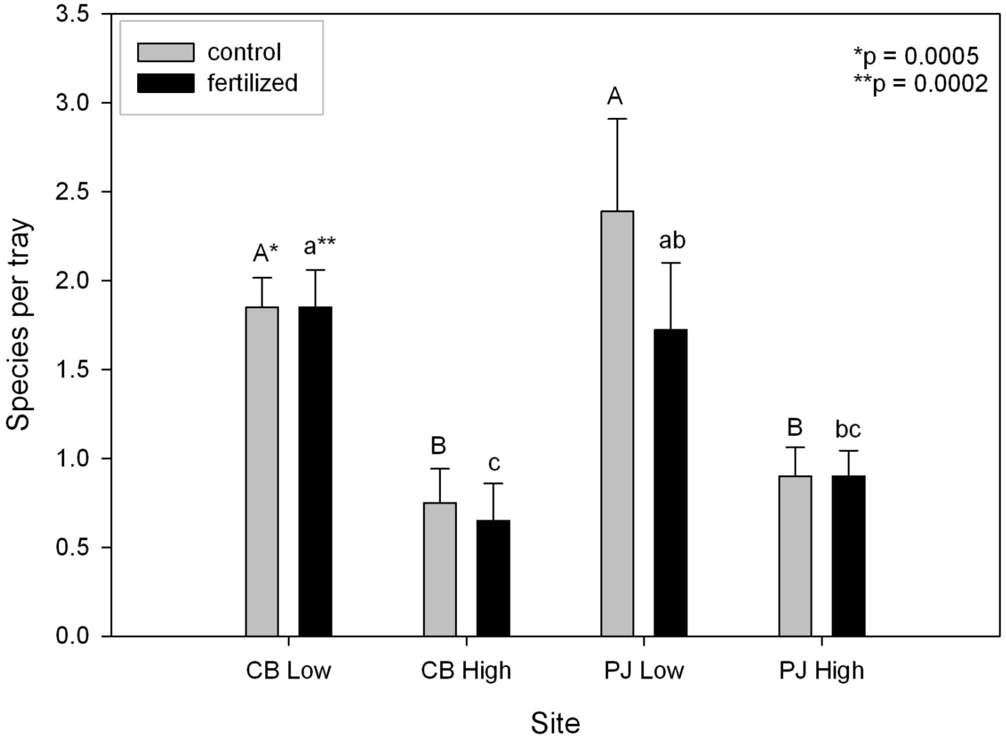

Table 1.7. Sørensen's similarity index for seed bank species composition between nitrogen treatments within sites and between nitrogen treatments among sites.

Comparisons	**Treatments**	
Within sites	Control vs. Fertilized	
PJ Low	46.2%	
PJ High	50%	
CB Low	40%	
CB High	54.5%	
Among sites	**Control**	**Fertilized**
PJ Low vs. PJ High	33.3%	25%
CB Low vs. CB High	54.5%	40%

Table 1.8. Linear regressions for relationships between invasive and native seed bank and field plant densities in control and fertilized treatments for creosote bush and pinyon-juniper vegetation in high and low nitrogen deposition sites for 2006 (prior to soil seed bank collection) and 2008 vegetation. Slopes that were significantly different from zero (denoted by *) were determined using $p < 0.05$. Ratios higher than 1 indicate higher density in the field than in the seed bank and ratios lower than 1 indicate higher seed bank density.

	Site – Nitrogen treatment	**Average Native field density Plants/m^2**	**Average Native seed bank density/m^2**	**Native Field : Seed bank density**	**Native R^2, p-value**	**Average Invasive field density Plants/m^2**	**Average Invasive seed bank density/m^2**	**Invasive Field : Seed bank density**	**Invasive R^2, p-value**
2006	PJ Low – control	10.3	381.9	0.03	0.001, 0.895	11.9	597.3	0.02	0.40, 0.005*
	PJ Low – nitrogen	15.2	340.3	0.04	0.06, 0.319	42	284.7	0.15	0.18, 0.079
	PJ High – control	34.5	37.5	0.92	0.33, 0.008*	216	1212.5	0.18	0.23, 0.032*
	PJ High – nitrogen	13.7	25	0.55	0.07, 0.268	181.5	1350	0.13	0.12, 0.138
	CB Low – control	112.1	137.5	0.82	0.09, 0.209	299.8	1593.8	0.19	4.16x10^{-5}, 0.979
	CB Low – nitrogen	47.2	181.3	0.26	0.08, 0.215	316.7	1731.3	0.18	0.05, 0.363
	CB High – control	27.9	56.3	0.50	0.03, 0.454	13.2	1075	0.01	0.18, 0.059
	CB High – nitrogen	18.8	25	0.75	0.07, 0.262	40.6	1250	0.03	0.24, 0.027*
2008	PJ Low – control	60.2	381.9	0.16	7.7x10^{-5}, 0.972	34.3	597.3	0.06	0.05, 0.362
	PJ Low – nitrogen	61.4	340.3	0.18	0.03, 0.489	33.2	284.7	0.12	0.24, 0.037*
	PJ High – control	46.2	37.5	1.23	2.5x10^{-5}, 0.983	139.3	1212.5	0.11	0.14, 0.107
	PJ High – nitrogen	31.3	25	1.25	0.02, 0.551	159	1350	0.12	0.08, 0.234
	CB Low – control	142.8	137.5	1.04	0.01, 0.647	52	1593.8	0.03	0.05, 0.325
	CB Low – nitrogen	81.4	181.3	0.45	0.24, 0.028*	54.1	1731.3	0.03	0.04, 0.428
	CB High – control	117.9	56.3	2.09	0.04, 0.397	34	1075	0.03	0.02, 0.552
	CB High – nitrogen	80.1	25	3.20	0.006, 0.742	34.5	1250	0.03	0.21, 0.040*

Table 1.9. Invasive percent cover in control and nitrogen fertilized plots from 2005. Significant differences were determined using a Kruskal-Wallis test ($p < 0.05$; denoted by *). CB = creosote bush, PJ = pinyon-juniper, Low = low N deposition site, and High = high N deposition site.

Site & Treatment	Mean % cover (SE)	H-value	p-value
CB Low Control	47.4 (3.2)	11.3	0.0008*
CB Low Fertilized	71.5 (4.1)		
CB High Control	27.3 (4.0)	0	1
CB High Fertilized	30.5 (6.4)		
PJ Low Control	15.8 (3.8)	0.21	0.6463
PJ Low Fertilized	19.3 (4.9)		
PJ High Control	31.9 (3.6)	6.6	0.0102*
PJ High Fertilized	53.1 (5.6)		

Chapter 2. Germination responses of native and invasive species to elevated soil nitrogen in deserts

Abstract

The effects of anthropogenic nitrogen deposition on aboveground vegetation are well studied. However, the repercussions of increased soil nitrogen for seed germination have not been well studied in natural systems. Native winter annuals make up a large portion of California's desert ecosystems and exist solely as seeds in the soil for most of the year. The impacts of increased soil nitrogen on seed germination could have significant effects on individual species abundance and community composition. The objective of this study was to determine the effects of elevated soil nitrogen on seed germination of native and exotic annual species found in California's deserts. Seeds of three native and three invasive winter annuals that are commonly found in the Colorado Desert were used in this study. Seeds were treated with 0, 2.5, 5, 10, 20, or 40µg N/g soil using ammonium nitrate solutions, and germination percentage and days to germination were recorded. The concentrations of nitrogen tested exceed the highest values observed in field soils under nitrogen deposition, but the highest concentration was also tested to show the potential range of responses. There were no effects of any of the nitrogen treatments within species; however, there were differences among species. *Bromus madritensis* ssp. *rubens* demonstrated nearly 100% germination under all nitrogen treatments, whereas *Salvia*

columbariae and *Schismus barbatus* had relatively low germination rates. The experiment shows that the high amounts of nitrogen found in some desert soils are likely not affecting the relative abundance of native vs. invasive annuals via germination, but other factors such as growth response to soil nitrogen may be involved.

Introduction

The effect of nitrogen on seed germination is well studied in agricultural systems (Fawcett and Slife 1978, Goudey et al. 1988, Dyer 1995, Brainard et al. 2006, Sweeney et al. 2008). However, the effect of increased soil nitrogen on seed germination in natural systems is less well understood. Southern California is subject to the highest levels of anthropogenic nitrogen deposition in the country (Fenn et al. 2003), due in part to high levels of urbanization, land use change, and the burning of fossil fuels. The western edge of the Sonoran Desert, known in California as the Colorado Desert, is affected by nitrogen deposition from Los Angeles and increased soil nitrogen levels have been measured near Palm Springs (Fenn et al. 2003). In low nutrient environments such as California's deserts, increased soil nitrogen can alter aboveground plant dynamics such as percent cover, density, and biomass (Brooks 2003, Allen et al. 2009). Changes in soil nitrogen can also affect seed germination (Mayer and Poljakoff-Mayber 1989, Baskin and Baskin 2001). Native winter annuals can make up 40% of the desert plant community (Kemp 1989) and yearly germination from the seed bank determines their aboveground species composition. Annual species relying on seed banks typically have specialized germination requirements and aboveground species composition is dependent on environmental cues that select for germination of certain species. As anthropogenic nitrogen deposition continues to affect Southern California and urbanization continues to spread towards the desert, it is important to understand how increased soil nitrogen may be affecting native and invasive species seed germination in nature.

Nitrogenous compounds (such as NO_3^-, NH_4^+, NO_x) are well-known germination stimulants (Hendricks and Taylorson 1974, Fawcett and Slife 1978, Bouwmeester and Karssen 1989, Pons 1989, Keeley and Fotheringham 1997, Egerton-Warburton 1998). However, germination responses to nitrogen can be species specific (Fawcett and Slife 1978, Monaco et al. 2003, Luna and Moreno 2009) and excess soil nitrogen has been shown to occasionally inhibit germination either directly, due to ammonia volatilization, or via soil acidification (Evenari 1949, Toole et al. 1956, Goudey et al. 1988, Bremner and Krogmeier 1989, Fenn et al. 1996, Roem et al. 2002). Here, I set out to determine how germination responses to elevated soil nitrogen differed by species and also by functional group to ascertain whether germination of exotic invaders would be more or less affected by increased nitrogen than native annuals.

Exotic invasive species are a problem throughout California and have altered the face of many of California's native ecosystems. Invasion in the desert is historically more recent (Brooks 1999, Minnich and Sanders 2000) than in most of California. The combination of the desert's harsh conditions and relatively recent urbanization may have allowed the desert to temporarily escape the scourge of invasive species. However, in the mid-20th century, exotic invasive annual grasses and forbs began to dominate the landscape (Minnich 2008). These invaders have had detrimental consequences to the native plant community by competing for water and nutrients (Brooks 2000b, 2003, Salo et al. 2005), as well as increasing fuel loads and fire frequency (Brown and Minnich 1986, Lovich and Bainbridge 1999, Brooks et al. 2004, Rao 2008, Steers 2008, Rao et al. 2010). Frequent, intense fires are historically rare in the California deserts (Brown and Minnich 1986, Brooks 1999) due to low biomass production and widely spaced perennials. Invasive annual species have the ability to increase shrub connectivity by leaving a persistent fine fuel layer between shrubs, leading to more frequent and widespread fires, which can act as a positive feedback for invasives (Brown and Minnich 1986, Brooks et al. 2004, Brooks and Minnich 2006, Rao 2008, Rao et al. 2010). If the germination of invasive species is stimulated or less inhibited by increased soil nitrogen than native annual forb germination, this could provide further evidence for the role of anthropogenic nitrogen deposition in the degradation of desert ecosystems.

Disruption of seed germination patterns due to elevated soil nitrogen is potentially detrimental to native plant populations. While it is possible for increased nitrogen to have a positive effect on native annuals, it is unlikely that exotic invaders would be negatively affected or that this positive response of natives would overcome the rapid germination and growth of invasive species. Given that weed species tend to germinate earlier and in higher numbers than native annuals (Steers and Allen 2010), enhanced germination of invasives could further degrade native habitats. Furthermore, germination of Sonoran Desert winter annuals may be density dependent. Thus, high invasive species seed output combined with the early and rapid phenology of invasive species could suppress germination of natives and force them to remain in the soil seed bank (Inouye et al. 1980) by exerting propagule pressure and altering the red – far red ratio, which affects seed germination (Yaniv et al. 1967, Salo 2004, Fenner and Thompson 2005, Pezzani and Montana 2006).

The purpose of this study was to determine how elevated soil nitrogen affects the germination of three native annual forbs and three invasive annual species found in the Colorado Desert. I hypothesized that invasive species would be less sensitive to increases in soil nitrogen than natives. Since many weed species are ruderal species in their native ranges, they often have lower dormancy than native desert annuals, which are adapted to conservative germination and seed banking (Baker 1974).

Methods

Study species

Six annual species were chosen for this study (Table 1). Three native annual forb species, *Amsinckia tessellata*, *Lepidium lasiocarpum*, and *Salvia columbariae*, and three exotic annual species, *Bromus madritensis* ssp. *rubens*, *Erodium cicutarium*, and *Schismus barbatus* were used in this study, all of which are found in the Colorado and Mojave deserts of Southern California. Since native annual forbs make up the largest proportion of the winter annual community and native annual grasses are less common, all of the native species tested were annual forbs. However, exotic annual grasses are common and make up two-thirds of the exotic invasive species used in this study. Mature seeds were collected by hand from populations growing in creosote bush scrub communities in the Colorado Desert in Joshua Tree National Park. All of the seeds of a single species were collected in May-June 2008 from one location within about 1 ha and seeds from multiple plants were combined into one bag. Seeds were stored in paper bags at room temperature in a lab at the University of California, Riverside.

A. tessellata (Boraginaceae), *L. lasiocarpum* (Brassicaceae), and *S. columbariae* (Lamiaceae) each form a basal rosette after germination and produce a flowering stalk at maturity. Seed mass was determined in the lab from field-collected seed (Table 1) to approximate species averages. Seeds were weighed individually or in lots, depending on the weight of single seeds. Some, but not all of the seeds used for average seed mass were used in the germination experiment.

The exotic invasive species used in this study, *B. madritensis*, *S. barbatus*, and *E. cicutarium*, were chosen because they are common invaders in the deserts of California. All three represent early-successional or ruderal species in their native ranges, but have experienced benefits of relocation that have led them to form stable communities and, in some cases, near monocultures in semi-arid California ecosystems (Brooks 2003, Brooks and Berry 2006, Allen et al. 2009).

B. madritensis and *S. barbatus* (Poaceae) are both invasive annual grasses native to the Mediterranean Basin (Minnich and Dezzani 1998, Brooks 2000a, c). *B. madritensis*, also known as red brome or foxtail chess, arrived in California in the mid to late 1800s (Minnich and Dezzani 1998), became common in the Mojave by the 1950s and spread to other deserts shortly thereafter (Brooks 2000a). *B. madritensis* is highly competitive with native annuals due to its early and rapid phenology and prolific production of highly germinable seeds (Brooks 1998, Brooks 2000a, Brooks 2000b). Seeds are capable of germination after a scant 1cm of precipitation, which is roughly half of the amount required for most native desert annuals (Beatley 1966). The seeds of *B. madritensis* are large (avg. 1.88mg) relative to most native annuals, are not long-lived in the soil seed bank (Salo 2004), and exhibit nearly 100% viability at maturity with only 2% carry over for future seasons (Wu and Jain 1979). Seed dormancy has been estimated to be only 2-3 years (Brooks 2000a). Since *B. madritensis* does not rely on long term seed banks as a source of reproductive insurance, it must rely on high seed dispersal by animals and humans (long-distance) and wind (short-distance) to hedge its bets in space by utilizing favorable microsites (Brooks 2000a, Salo 2004). It is also highly nitrophilous in growth compared to native forbs (Brooks 2003, Allen et al. 2009) and has higher survival rates than native annuals (Beatley 1966), making it a strong competitor. However, *B. madritensis* is susceptible to ‘boom and bust’ cycles between dry and wet years due to its lack of persistent seed banks during drought (Brooks 2000a, Salo 2004).

S. barbatus, also called Mediterranean grass or split grass, is native to the Mediterranean Basin and the deserts of Africa and the Middle East (Jackson 1985, Minnich and Dezzani 1998). It was introduced to California during the middle of the 20th Century (Minnich and Dezzani 1998, Brooks 2000c) and is commonly found in the low elevation desert (less than 1300m) in California. Like *B. madritensis*, *S. barbatus* requires about 1cm of precipitation to stimulate germination (Brooks 2000c), however it is better adapted to surviving drought conditions than *B. madritensis*. *S. barbatus* is an effective competitor for soil nutrients and can have detrimental effects on native plant communities (Brooks 1998, Brooks 2000b, 2003). The seeds of *S. barbatus* are extremely small (avg. 0.08mg), translucent, and resemble grains of sand. Seeds of *S. barbatus* are dispersed by sheet flooding and wind (Brooks 2000c), as well as ants (Rissing 1986). Capable of reaching reproductive maturity in as little as two weeks, *S. barbatus* is one of the fastest maturing desert plants (Brooks 2000c). Unlike *B. madritensis*, *S. barbatus* is capable of creating a soil seed bank. Only a fraction of the seed bank germinates each year, thereby utilizing a similar bet-hedging strategy as that of native desert annuals (Gutterman 1994) and giving it a competitive advantage compared to *B. madritensis* by evading drought in time.

E. cicutarium (Geraniaceae), also known as filaree or storksbill, is a basal rosette-forming invasive annual forb that is native to Mediterranean Europe (Minnich and Dezzani 1998). There is some debate as to when and how *E. cicutarium* arrived in California and spread to the desert, but it likely arrived prior to Spanish settlement and was widespread throughout the state by the mid 1800s (Mensing and Byrne 1998, Minnich 2008). There is one closely related native congener in the California deserts, *Erodium texanum*. *E. cicutarium* has a cosmopolitan distribution throughout the USA and is a common invader in many of California’s ecosystems. *E. cicutarium*, like many invasive species, has an early and rapid phenology and benefits from high seed output. The presence of a hard, impermeable seed coat confers an added advantage by allowing *E. cicutarium* to form a persistent soil seed bank (Harper 1977, Roberts 1981, Mayor et al. 1999). *E. cicutarium* is able to store high numbers of seeds in the soil and uses two simultaneous dormancy states (exogenous and endogenous) to prevent synchronized germination and subsequent seed bank depletion (Mayor et al. 1999). The ability to create seed banks allows populations to remain fairly stable over time. Germination rates are lower than some other ruderal species (Mayor et al. 1999) and seeds of *E. cicutarium* can remain viable for at least 35 years after dispersal (Hull 1973), making it a long-term competitor in both time and space.

Germination requirements

Four of the species used in this study did not require any seed treatments prior to germination. Seeds of *B. madritensis*, *S. barbatus*, *L. lasiocarpum*, and *S. columbariae* are all capable of successful germination without any specialized pre-treatment. The awns were removed from *B. madritensis* for easier handling, but this does not affect germination. However, seeds of *A. tessellata* and *E. cicutarium* did require treatment prior to germination. *A. tessellata* has a hard teardrop-shaped seed that was clipped prior to germination to increase water uptake by the seed. *E. cicutarium* has a hard, impermeable seed coat as well as two types of seed dormancy (Mayor et al. 1999) and required a combination of treatments to stimulate germination. After several germination trials in the laboratory, I found the highest levels of germination after treating *E. cicutarium* by chilling the seeds at 7°C, clipping the seed tip, and then soaking the seeds in a 0.04g/L gibberellic acid solution. Seeds of all species were thoroughly cleaned to remove any extraneous flower parts from the seeds.

Experimental procedures

Seeds were germinated in soil collected from the intershrub spaces at a creosote bush scrub site in Joshua Tree National Park with low nitrogen deposition rates. Germination trials were conducted prior to experimental set up to ensure that the seeds were viable. Total carbon and nitrogen content of the soil was measured using a Thermo-Finnigan Flash A1112 soil combustion N/C analyzer system. Total soil carbon and nitrogen were 0.14 and 0.01%, respectively. Total extractable nitrogen (NH_4^+, NO_3^-) prior to applying fertilization treatments was 5.4μg/g. The soil was autoclaved to kill any unwanted seeds residing in the soil. Seeds were germinated in Petri dishes filled with soil 1cm deep. Species were germinated separately with 10 seeds of a single species per Petri dish. Six nitrogen treatments (0, 2.5, 5, 10, 20, 40μg N/g soil added) were applied with five replications for a total of 180 Petri dishes using a complete randomized design. The nitrogen treatments were chosen to create a range from field conditions (0N added) to a simulated high deposition scenario (40μg N/g soil added). Currently, 40μg N/g soil exceeds actual soil nitrogen concentrations in high deposition sites (Allen et al. 2009, Rao et al. 2009), which can be up to 30 μg N/g soil in the Colorado Desert, but was chosen to simulate future soil nitrogen levels under increasing deposition. Nitrogen was applied as ammonium nitrate solution. The Petri dishes were placed on a lab bench in a temperature-controlled room with natural light at the University of California, Riverside. Air conditioning maintained the temperature between 21-27°C to simulate winter field conditions in the low desert and the seeds received natural sunlight through windows and skylights. The germination experiment was conducted from July through November 2009. The Petri dishes were kept moist with deionized water, as needed, and rotated weekly across the lab bench to prevent position-related effects. Successful germination was defined as radicle emergence from the seed. As seeds germinated, the date was recorded and the seed was removed from the Petri dish. Seeds that failed to germinate were not tested for viability at the end of the study. The experiment concluded when germination ceased for over two weeks.

Data analysis

There are many germination indices that can be used to characterize germination data; however, many of these indices are flawed and can lead to ambiguous results (Brown and Mayer 1988). Therefore, total germination data was used in these analyses. Total germination per Petri dish was recorded and calculated as a germination percentage per Petri dish. Data were analyzed by nitrogen treatment within species, as well as among species. The date of germination was also recorded for individual seeds, which was used to calculate total number of days to germination per Petri dish. The length of germination time was also compared within and among species. Data were non-normal and analyzed using the Kruskal-Wallis test for nonparametric data. Arcsine transformations are common in germination analyses (Scott et al. 1984), however much of the data resisted transformation and nonparametric analysis was used in lieu of transformation. Significant differences were detected using Tukey's HSD and $\alpha = 0.05$.

Results

There was no effect of nitrogen on percent germination within species, with the exception of *E. cicutarium* (Table 2). Percent germination by nitrogen across species differed at all nitrogen levels (Figure 2; Table 3). *B. madritensis* had the numerically highest germination percentage in each nitrogen treatment, while *S. columbariae* had consistently low germination, although these species were not always different from all others. Germination was the most similar between species at the 10 and 20µg/g nitrogen levels, with only *S. columbariae* being significantly different from the others. Species exhibited the biggest differences in germination at the lowest (0 and 2.5µg/g) and highest (40µg/g) nitrogen levels.

Days to germination were affected by nitrogen only for *A. tessellata* (Figure 1; Table 2). For all other species, days to germination did not differ between nitrogen treatments. Differences in days to germination between species were significant at every nitrogen level (Figure 3; Table 3). Lower mean days for days to germination indicate fast germination of seeds. *S. columbariae* had consistently low number of days to germination, but this is likely due to low germination overall rather than faster germination relative to other species. *A. tessellata* and *S. barbatus* had consistently long germination periods, while *E. cicutarium* and *S. columbariae* typically took fewer days to germinate. No functional group patterns were detected, likely due to the fact that the invasive species in this experiment possess different germination strategies (see species descriptions in methods section).

Discussion

In this study, percent seed germination was not dependent on soil nitrogen level for individual species, which contradicted my hypothesis. This finding is surprising given that nitrogenous compounds, such as nitrate, are well established as germination stimulants (Hendricks and Taylorson 1974, Pons 1989, Keeley and Fotheringham 1997, Henig-Sever et al. 2000). Responses to nitrogen can be species specific (Fawcett and Slife 1978, Monaco et al. 2003, Luna and Moreno 2009) and dependent on the nitrogen concentration used (Goudey et al. 1988). Monaco et al. (2003) found that non-dormant seeds of the exotic invasive grasses *Bromus tectorum* and *Taeniatherum crinitum* were not affected by increased soil nitrogen. This pattern held true for the invasive grass *B. madritensis* in this study, which demonstrated 90 – 100% germination in all treatments. *E. cicutarium* and *S. barbatus*, the other two invasive species used in this study, demonstrated lower germination percentages than *B. madritensis*, which reinforces the fact that these seeds use different bet-hedging strategies than *B. madritensis* and that they possess dormancy mechanisms (Harper 1977, Mayor et al. 1999, Brooks 2000c). The conservative germination of *Schismus* species was demonstrated in a study by Gutterman, where germination ranged between 14 – 21.5% at room temperature over 20 days (1994). In this study, *S. barbatus* exhibited higher germination rates, roughly 45 – 80%, but was still relatively more conservative than the non-dormant *B. madritensis*. These differences demonstrate two different life strategies used by these invaders. *S. barbatus* "hedges its bets" in time and space by utilizing fractional germination and seed banking, similar to native annuals, but it also has the advantage of a very rapid growth rate. *B. madritensis* exhibits traits similar to Baker's ideal weed (Baker 1974) by producing high numbers of large, readily germinable seeds. While this strategy can lead to rapid invasion in years with adequate precipitation, it also makes *B. madritensis* susceptible to population crashes in periods of sustained drought.

The consistently low germination of *S. columbariae* under all treatments was surprising due to its generally high germination rates under laboratory conditions (H. Schneider personal observation). The highest percent germination of *S. columbariae* achieved in this study was 20%, which was lower than other species for almost every treatment level. It is unclear why *S. columbariae* germination was unexpectedly low, but it could be related to seed storage prior to germination, unfavorable temperature or light conditions in the laboratory, or a negative response to autoclaved soil. In an attempt to remedy any detrimental influences of autoclaved soil, the *S. columbariae* germination trials were repeated with untreated soil, which did not improve germination.

While the differences within species were not significant in most cases, the differences between species were significant. However, because the changes in relationships between species were not always significant, I cannot attribute them to the nitrogen treatments. These results suggest that soil nitrogen may not be as important as inherent germination differences between these species. However, germination responses to nitrogen can be species specific (Fawcett and Slife 1978, Monaco et al. 2003, Luna and Moreno 2009) and it is hard to predict how other native desert annual species would respond to increases in soil nitrogen. Furthermore, laboratory germination studies are limited by the artificial nature of the setting and this study may be affected by the relatively small sample size that was used. Repeating the experiment and increasing the sample size would strengthen these results. Additionally, recording detailed field collection data, such as precipitation, maternal plant size, and maternal fecundity, could help to account for maternal effects, which can affect seed dormancy, dispersal, and germination traits (Roach and Wulff 1987, Philippi 1993). While laboratory studies provide some basic information about seed germination, field studies are also needed to determine whether nitrogen deposition has the ability to alter seed germination of desert annual plants. Follow-up studies to this one should include the species tested as well as additional, less-common species in order to more fully understand the effects of increased soil nitrogen on germination of native annuals.

Anthropogenic degradation of Southern California's deserts has altered ecosystems and is a threat to native plant species (Lovich and Bainbridge 1999). Increased soil nitrogen can affect seed germination (Goudey et al. 1988, Roem et al. 2002, Sweeney et al. 2008) and may create a negative feedback for annual species that form soil seed banks (Plassmann et al. 2008). However, nitrogen did not have a strong effect on seed germination in this study. Understanding how increased soil nitrogen affects seed germination could be important for identifying species-specific effects of nitrogen deposition and may be used to inform habitat conservation and restoration plans where seed germination responds to nitrogen.

It is likely that the Colorado Desert will continue to be affected by anthropogenic nitrogen deposition in the future. The potential aboveground effects of nitrogen deposition in the desert have been thoroughly investigated in the last decade (Brooks 2003, Fenn et al. 2003, Allen et al. 2009), but the effects of deposition on seed germination in natural lands are less well understood (but see (Plassmann et al. 2008). In this study using realistic concentrations of soil nitrogen found in high deposition sites, there were no effects of nitrogen on germination. This suggests the dominance of invasive species in high deposition areas is not determined by differential germination. Instead, dominance of exotic invasive species may be affected by their positive growth response to elevated nitrogen compared to native species (Rao and Allen 2010).

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Table 2.1. Functional group and family of native and exotic study species and average seed mass.

Functional Group	**Family**	**Species**	**Average seed weight (mg)**
Invasive annual grass	Poaceae	*Bromus madritensis* ssp. *rubens*	1.88
		Schismus barbatus	0.08
Invasive annual forb	Geraniaceae	*Erodium cicutarium*	1.57
Native annual forb	Boraginaceae	*Amsinckia tessellata*	3.04
	Brassicaceae	*Lepidium lasiocarpum*	0.425
	Lamiaceae	*Salvia columbariae*	1.01

Table 2.2. H-values and p-values based on Kruskal-Wallis test for nonparametric data for effects of N fertilizer on percent germination and days to germination for each species (means in Figure 2). Significance is denoted by * and was determined by a Tukey's HSD using $\alpha = 0.05$, df = 5.

	Percent germination		**Days to germination**	
Species	**H-value**	**p-value**	**H-value**	**p-value**
Amsinckia tessellata	9.7743	0.0819	17.2143	0.0041*
Bromus madritensis ssp. *rubens*	2.2199	0.818	2.0143	0.8472
Erodium cicutarium	1.3915	0.9252	9.9556	0.0765
Lepidium lasiocarpum	7.4824	0.1872	6.1737	0.2897
Salvia columbariae	10.957	0.0522*	2.7578	0.7373
Schismus barbatus	6.3692	0.2719	2.1979	0.8211

Figure 2.1. Days of germination within species across nitrogen levels using a Kruskal-Wallis test for nonparametric data. Significant differences were determined using α = 0.05, df = 5. Treatments within a species separated by different letters are significantly different.

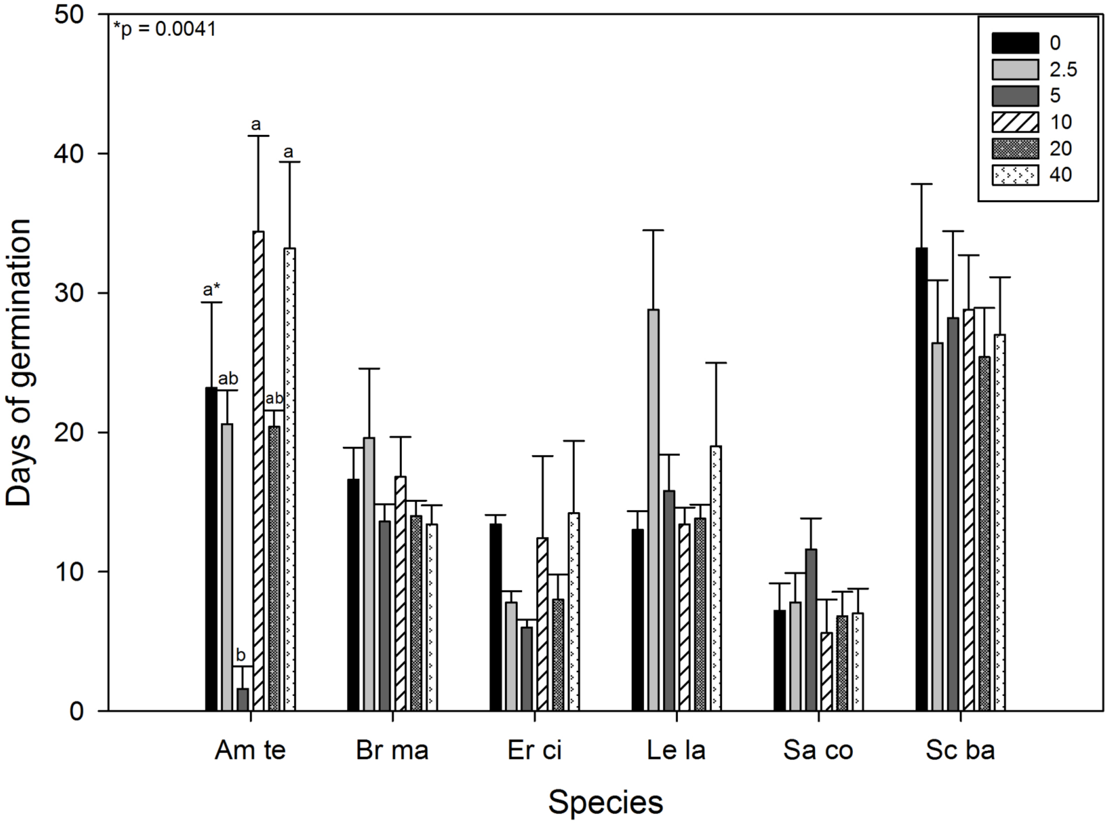


Table 2.3. H-values and p values (df = 5) based on Kruskal-Wallis test for differences in percent germination (means in Figure 1) and days to germination (means in Figure 3) among species within each N fertilizer level. Significance is denoted by *. Tukey's HSD was used to detect significant differences using α = 0.05, df = 5.

	Percent germination		**Days to germination**	
Nitrogen level (ppm)	**H-value**	**p-value**	H-value	p-value
0	17.638	0.0034*	20.8396	0.0009*
2.5	20.1905	0.0012*	19.6363	0.0015*
5	20.1206	0.0012*	22.4835	0.0004*
10	18.3533	0.0025*	18.6906	0.0022*
20	18.0621	0.0029*	24.0375	0.0002*
40	22.0117	0.0005*	17.365	0.0039*

Figure 2.2. Percent germination under multiple nitrogen treatments among species Means separated by different letters within nitrogen levels and across species are significantly different using a Kruskal-Wallis test for nonparametric data and Tukey's HSD ($\alpha = 0.05$).

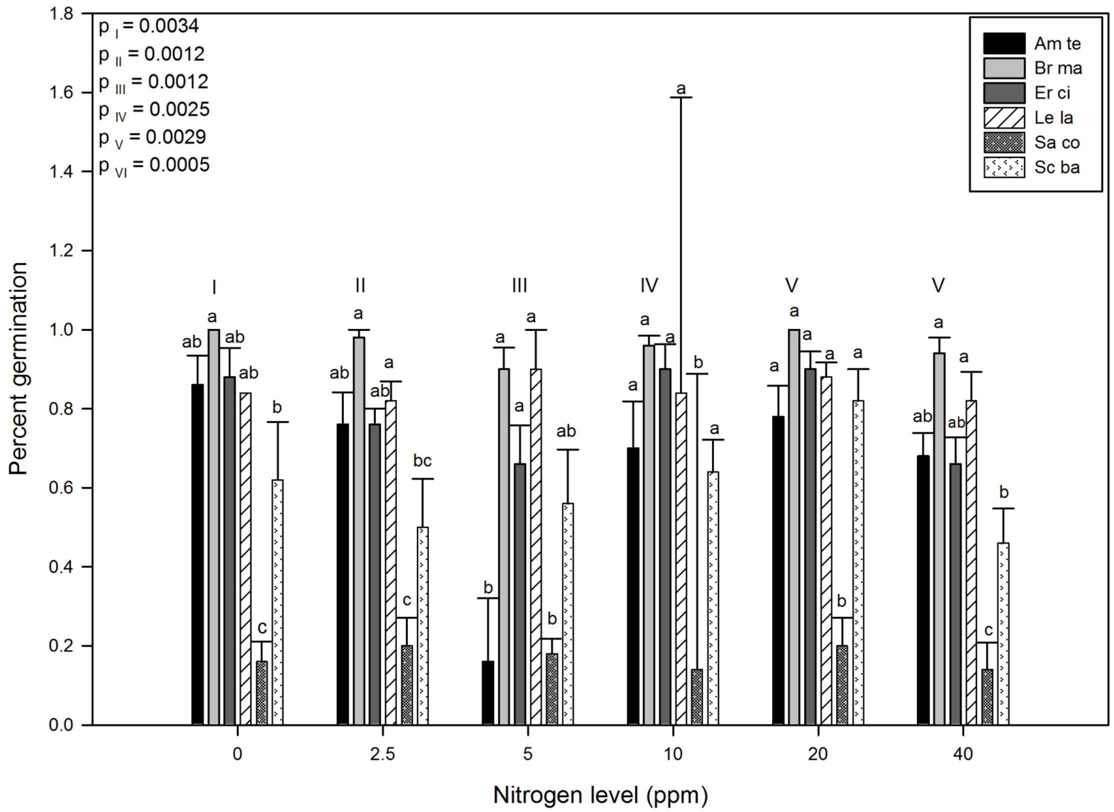
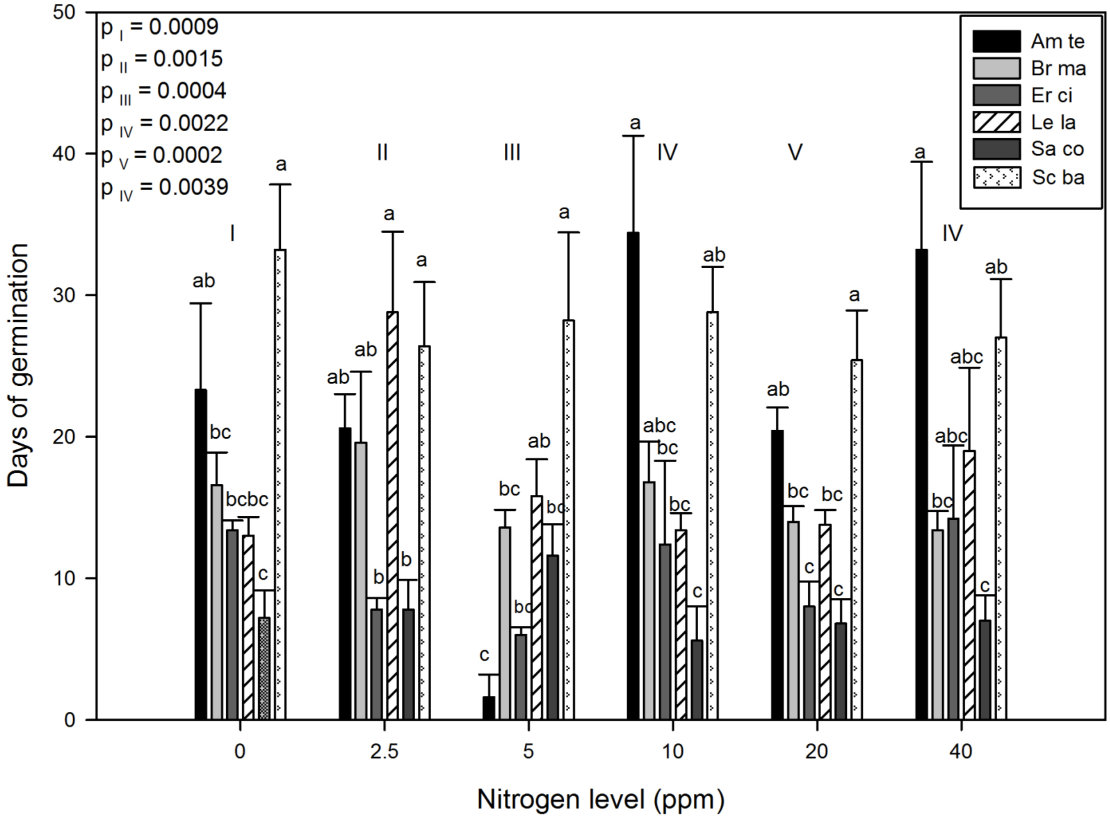


Figure 2.3. Days of germination among species by nitrogen level using a Kruskal-Wallis test for nonparametric data. Significant differences were determined using α = 0.05, df = 5. Treatments within a species separated by different letters are significantly different.



Chapter 3. *Erodium cicutarium*, an invasive desert annual forb, experiences increased benefits of water and nitrogen over native annual forbs

Abstract

Anthropogenic nitrogen deposition acts as an artificial fertilizer enhancing soil nitrogen levels in the otherwise nutrient-poor deserts of Southern California. Exotic invasive species are often more nitrophilous than native desert species, which are adapted to low nutrient soils. This can create a nitrogen deposition-invasive species feedback loop, where invasives benefit from increases in soil nitrogen more than native species. Here, a greenhouse experiment evaluated the effects of six nitrogen levels (0, 2.5, 5, 10, 15, 20 mg N kg^{-1} soil) and two watering treatments (20% and 60% free drainage) on the growth of one invasive and three native annual forbs common to the Colorado Desert. The high water treatment (60%) typically led to significantly larger increases in plant growth than the 20% watering treatment, highlighting the fact that this system is primarily water-limited. Although both native and invasive annuals experienced benefits of nitrogen additions, the invasive forb *Erodium cicutarium* demonstrated more consistent increases in growth and reproductive effort with each successive increase in nitrogen. For example, *E. cicutarium* basal rosette width doubled from the 0 mg N kg^{-1} soil, 20% water treatment to the 20 mg N kg^{-1} soil, 60% water treatment, suggesting that aboveground competition could intensify under high water and high nitrogen inputs. Annual forbs tended to

experience maximum growth benefits at intermediate levels of nitrogen additions, such as 10 or 15 mg N kg^{-1} soil. Percent tissue nitrogen concentration measurements showed the most similarity between the invasive and native species compared to other measured responses, with all species increasing in tissue nitrogen concentrations up to the highest soil nitrogen level. The ability of *E. cicutarium* to utilize soil nitrogen additions in a stepwise fashion suggests that it has the ability to be a dominant competitor in the desert, especially under high nitrogen deposition. Habitat conservation and restoration efforts should focus on areas of high nitrogen deposition, where *E. cicutarium* is most likely to have severe competitive effects on natives.

Introduction

Desert winter annual plants are adapted to survival in harsh, unpredictable environments (Mulroy and Rundel 1977, Werk et al. 1983, Pake and Venable 1996, Smith et al. 1997, Venable 2007). Arid ecosystems are limited by water and often regulated by nitrogen (Noy-Meir 1973, Hooper and Johnson 1999, Krueger-Mangold et al. 2004, Snyder et al. 2004). Nutrient allocation in annuals often favors reproduction to ensure species survival into future growing seasons (Williams and Bell 1981) and total biomass can vary annually depending on the amount and timing of precipitation (DeFalco et al. 2001, Schwinning and Ehleringer 2001, James et al. 2006, Rao and Allen 2010).

In California's deserts, increasing nitrogen deposition is altering soil nutrient availability (Fenn et al. 2003a, Fenn et al. 2003b, Allen et al. 2009, Rao et al. 2009, Fenn et al. 2010) and may be altering the growth and nutrient allocation of winter annual forbs. In low-nitrogen soils, such as those found in California's deserts, even low levels of nitrogen deposition can elicit a positive response from annual forbs (Brooks 2003, Chambers et al. 2007, Clark and Tilman 2008, Rao and Allen 2010, Rao et al. 2010). As urbanization and agriculture surrounding the desert continue to expand, nitrogen deposition will likely increase as well.

Another factor altering California's deserts is the impact of exotic invasive annual plant species, which have the ability to compete with native plants for soil water and nutrients (Brooks 2000b, Brooks 2000c, a, DeFalco et al. 2003, Rodriguez-Buritica and Miriti 2009). Several studies have shown that, in addition to having negative impacts on native ecosystems, invasive species in the desert can benefit from increases in soil nitrogen (Brooks 2003, James et al. 2006, Allen et al. 2009, Rao and Allen 2010) and that nitrogen deposition may aid in the dominance of invasives in some areas (Huenneke et al. 1990, Brooks 2003, Chambers et al. 2007). Native annual forbs in the desert are adapted to cope with low nutrient soils and have variable responses to nitrogen additions (Williams and Bell 1981, Werk et al. 1983, Schwinning and Ehleringer 2001, Allen et al. 2009, Rao and Allen 2010). Although nitrogen additions can enhance competition between native and invasive species (James and Richards 2006, James and Richards 2007), some studies have shown that this response may not occur when invasive species occur in low densities (Schneider ch. 4).

Finally, global climate change models predict that California's desert ecosystems will experience warmer temperatures and increasingly variable precipitation in the future

(Hayhoe et al. 2004, Weiss and Overpeck 2005). As California's deserts continue to experience changes in water and nutrient availability and competition from invasive species, studies investigating the effects of variable water and nitrogen availability can provide insight into desert annual plant responses.

A previous study found that *Bromus madritensis* ssp. *rubens* and *Schismus* spp., two desert invasive annual grasses, are capable of positively responding to increases in water and nitrogen and may be capable of producing biomass that exceeds fire thresholds under nitrogen deposition (Rao and Allen 2010). Furthermore, *Amsinckia tessellata*, a native winter annual forb, showed no response to nitrogen at low water levels and negative responses to nitrogen under high water levels (Rao 2008). In light of this knowledge, this study aimed to determine how three common native annuals forbs and one invasive annual forb would respond to variable soil nitrogen and water availability. *Cryptantha angustifolia*, *Lepidium lasiocarpum*, and *Salvia columbariae* are winter annual forbs native to creosote bush scrub communities in the Colorado Desert in California and *Erodium cicutarium* is a common invasive annual forb that co-occurs with native winter annual forb species. Using a combination of six nitrogen (0 nitrogen added to 20 mg N kg^{-1} soil) and two watering treatments (20% and 60% free drainage), I measured biomass and nitrogen allocation within and among species. I hypothesized that all species would be capable of responding positively to nitrogen, but that *E. cicutarium* would experience the most benefits because its growth strategy allows it to be resistant to water stress and respond positively to nitrogen additions (Peláez et al. 1995, Busso et al. 1998, Brooks 2003). Second, I hypothesized that all plants would experience the greatest benefits in high water treatments because desert annuals are primarily limited by water. Finally, I hypothesized that the interaction between water and nitrogen treatment would be significant because desert annuals cannot utilize increased nitrogen without sufficient soil moisture availability.

Methods

Greenhouse experimental design

The growth responses of native and invasive annual forbs were examined under multiple nitrogen and watering treatments in a greenhouse at the University of California, Riverside. Three species of native winter annual forbs were chosen for this study: *Cryptantha angustifolia* (Boraginaceae), *Lepidium lasiocarpum* (Brassicaceae), and *Salvia columbariae* (Lamiaceae). These species were chosen because they are common native annual forbs in creosote bush scrub communities in the Colorado Desert. *Erodium cicutarium* (Geraniaceae) is an exotic invasive annual forb that is also common in the creosote bush scrub communities in the desert. *E. cicutarium* was likely transported to California prior to the arrival of Spanish missionaries (Mensing and Byrne 1998) and is native to Mediterranean Europe and Africa (Minnich and Dezzani 1998). Seeds of *E. cicutarium*, *L. lasiocarpum* and *S. columbariae* were collected from many individuals in the Coachella Valley from creosote bush scrub communities. Naturally occurring seeds of *C. angustifolia* germinated from the field-collected soil used in this experiment and seedlings were utilized in this study. Seeds of *E. cicutarium* required treatment to stimulate germination and were chilled, clipped, and treated with a 0.04 gL^{-1} gibberellic acid solution prior to planting. The other three species germinated without any prior treatment of the seeds.

Soil for this experiment was collected from a site in Joshua Tree National Park that experiences low levels of nitrogen deposition (Pinto Basin with 3.4 kg N ha^{-1} yr^{-1}; Allen et al. 2009 and unpublished data). All four species used in this experiment naturally occur at the site where soil was collected. General physical soil characteristics at this site were determined in a previous study (Rao 2008). Soil percent sand-silt-clay were determined to be 83-13-4, with 13.9% gravel, 13.8 C:N, and a slightly alkaline pH of 8.37. Total soil carbon and nitrogen were measured using a Thermo-Finnigan Flash A1112 soil combustion N/C analyzer system at the University of California, Riverside. Total soil carbon was determined to be 0.138% and total soil nitrogen was 0.01%. Total extractable soil nitrogen (NH_4 plus NO_3) prior to fertilization was 5.42 mg N kg^{-1} soil.

Prior to planting, 1000 g of soil were added to 720 mL square 12.5 cm pots (Landmark Plastics, Akron, OH). Each pot was filled and weighed individually to ensure uniform amounts of soil. Germination tests were performed to determine the number of seeds required to ensure germination within pots. Multiple seeds were sown into each pot and eventually thinned and transplanted so that a single individual was growing in each pot.

Five nitrogen levels plus an untreated control (0, 2.5, 5, 10, 15, 20 mg N kg^{-1} soil) and two watering treatments (20% or 60%) were used in this study. These levels were chosen to encompass the variability of soil nitrogen and water availability within the Sonoran Desert (Rao et al., 2009, Rao and Allen 2010). Nitrogen levels vary due to soil type and exposure to nitrogen deposition, and water availability is dependent on annual precipitation. It is also possible that these two resources are co-limiting and that altering water availability could affect the ability of plants to utilize increased soil nitrogen.

The experiment was set up in a greenhouse at the University of California, Riverside with ambient temperature and light conditions. The average temperature during the study period ranged from a maximum of 23°C and a minimum of 7°C, conditions that occur in the field during the winter growing season (NOAA, http://lwf.ncdc.noaa.gov/oa/climate /stationlocator.html). The experiment was a full factorial design with seven replicates (6 N x 2 water x 4 species x 7 reps = 336 pots). The three native forb species were planted on November 21, 2008. The invasive forb, *E. cicutarium*, was added to the study later and was planted on October 19, 2009. Pots were completely randomized in the greenhouse and moved periodically to avoid possible temperature gradients. They were fertilized with liquid ammonium nitrate (NH_4NO_3) at one of the five aforementioned levels once seedlings were established. Pots were fertilized again approximately one month later to maintain soil nitrogen levels. Initial soil moisture was determined based on gravimetric water content of the pots at free drainage. The pots in the low watering treatment were maintained at 20% free drainage and pots in the high watering treatment were maintained at 60% free drainage by weight. Throughout the experiment, pots were weighed and watered using deionized water 3-4 times per week, depending on temperature and water loss per pot. Plants were measured and harvested by species when the majority of individuals reached peak biomass, which was characterized as peak flowering. Shoot biomass was harvested and dried in an oven at 60°C prior to being weighed. Harvest dates varied by species. *C. angustifolia* was the first species harvested on February 5, 2009. *L. lasiocarpum* was harvested on March 4, 2009 and *S. columbariae* on April 6, 2009. *E. cicutarium* was harvested on January 27, 2010. The tissue was then ground and tested for total carbon and nitrogen content using the same method as the soil. Roots were left in the pots, the soil was allowed to dry, and the pots were stored in a refrigerator until the roots could be washed, dried, weighed for root biomass, and analyzed for total root tissue carbon and nitrogen. Relative growth rate (RGR) was calculated as $(\ln M_f - \ln M_i)/(t_f - t_i)$, where M_i and M_f represent seed mass and final biomass (g) and t_f - t_i represents the number of days between planting and harvesting.

Soil samples were collected at the beginning of the experiment, after the second fertilizer application, and at the time of harvest to monitor soil extractable nitrogen levels. Extractable nitrogen (NH_4^+ and NO_3^-) was measured using a flow-injection analyzer at the University of California Division of Agriculture and Natural Resources Analytical Laboratory (danranlab.ucdavis.edu).

Data analysis

A two-way analysis of variance (ANOVA) was used to determine the effects of water and nitrogen treatments, as well as the interaction between the treatments, for normally distributed or transformed data (log or square root transformation). Data that resisted transformation were analyzed using a Kruskal-Wallis test for non-parametric data. Significant differences between treatments were determined using Tukey's Honestly Significant Difference (HSD) for more than two groups or Student's t-test when only two groups were being compared. If no interaction was found, the data were analyzed using a one-way ANOVA to determine nitrogen effects within each water treatment separately. Within species, I compared rosette width (*L. lasiocarpum*, *E. cicutarium*, and *S. columbariae*) or plant height (*C. angustifolia*), depending on species morphology. Number of flowers, root-to-shoot ratio (R:S) and tissue nitrogen content were also measured. Growth rate (GR) was calculated using seed weight and final total biomass.

All statistics were analyzed using JMP 8.0 statistical software package. Graphs were created using SigmaPlot graphing package.

Results

Individual species responses to water and nitrogen treatments

As predicted, both native and invasive species responses were the most dramatic under the 60% water treatment, which consistently conveyed an advantage over the 20% water treatment. Nitrogen responses were variable within species, although the midlevel nitrogen treatments (5-15 mg N kg^{-1} soil) frequently produced the highest biomass, tallest plants, and highest tissue nitrogen concentrations in all species except for *E. cicutarium*.

The interaction between water and nitrogen treatments was not significant for any species.

Shoot biomass

A 2-way ANOVA showed that *Cryptantha angustifolia* shoot biomass was affected by both water and nitrogen ($p = 0.0082$, <0.0001; respectively; Figure 1). In both watering treatments, the highest biomass produced represented three times that of the lowest biomass, reinforcing the lack of an interaction between water and nitrogen treatments. Shoot weight of *L. lasiocarpum* was affected by both water and nitrogen treatments ($p < 0.0001$, $p = 0.0021$; respectively), with the 60% H_2O treatment leading to higher biomass than the 20% H_2O (Figure 1). Nitrogen treatments were only different under 60% H_2O, with 15 mg N kg^{-1} soil allowing twice as much aboveground biomass production than 0 mg N kg^{-1} soil added (F-ratio = 4.3179, 5df, $p = 0.0035$).

Both water and nitrogen treatments were important for affecting total shoot biomass of *S. columbariae* individuals ($p < 0.0001$ for both factors; Figure 1), although a one-way ANOVA showed that the only differences due to nitrogen were found under 60% H_2O, where 0 mg N kg^{-1} soil led to the production of three times less biomass than 15 mg N kg^{-1} soil (F-ratio = 5.2007, 5df, $p = 0.0011$). *E. cicutarium* shoot biomass was increased by 60% H_2O and increased nitrogen fertilization ($p < 0.0001$ for both factors; Figure 1). *E. cicutarium* was the only species for which increased nitrogen always caused an increase in biomass.

Plant height, rosette width, and flower number

Due to growth form, *C. angustifolia* plant height was analyzed in lieu of basal rosette width, which was used for the other three species. Only watering affected the height of *C. angustifolia* plants (F-ratio = 4.49, 1df, $p = 0.0376$; Figure 2), with those grown under 60% H_2O averaging an extra centimeter of height. However, a Tukey's HSD did not differentiate any of the treatments for plant height or number of flowers.

In *L. lasiocarpum*, basal rosette width was also increased under 60% H_2O but was only significant for the 2.5 mg N kg^{-1} treatment ($p < 0.0001$). *L. lasiocarpum* individuals grown in pots that received 60% H_2O also had twice as many flowers as those that received 20% H_2O, but no differences due to nitrogen were detected (Figure 3).

S. columbariae rosette width was significantly increased under 60% H_2O, but was not affected by nitrogen treatments (Figure 2). Interestingly, under 60% H_2O, plants that received the 0 and 20 mg N kg^{-1} soil treatments produced the same number of flowers (Figure 3).

Benefits of increased nitrogen and water so strongly affected *E. cicutarium* growth that plants growing under 20 mg N kg^{-1} soil, 60% H_2O had basal rosettes that were twice as wide as with 0 mg N kg^{-1} soil, 20% H_2O and reached diameters of almost 11 cm (Figure 2). The number of flowers in 20 mg N kg^{-1} soil, 60% H_2O treated pots was over three times that of plants that received 15 mg N kg^{-1} soil (6.6 and 1.9, respectively, $H = 11.0743$, 5df, $p = 0.0499$; Figure 3).

Root:shoot, tissue nitrogen content, and growth rate

Nitrogen was the only significant factor affecting R:S in *C. angustifolia* individuals, with the 0 mg N kg^{-1} soil treatment having a higher R:S than any other nitrogen level (F-ratio = 9.672, 5df, $p < 0.0001$; Figure 4). Overall, *L. lasiocarpum* R:S was only affected by watering treatment, with the 20% H_2O treatment leading to consistently higher R:S than 60% H_2O (F-ratio = 7.0458, 1df, p = 0.0098; Figure 4), although Tukey's HSD found few significant differences between treatments. *S. columbariae* R:S was unaffected by either water or nitrogen treatments and was the only species to exhibit this type of strategy. On the other hand, *E. cicutarium* R:S was influenced by both water and nitrogen ($p < 0.0001$, p = 0.0164; respectively; Figure 4), but the only significant differences existed between the 20% and 60% watering treatments. For example, the highest R:S was measured in the 20% H_2O, 0 mg N kg^{-1} soil treatment and was roughly 50% higher than R:S in the 10 and 20 mg N kg^{-1} soil treatments receiving 60% H_2O.

Total tissue nitrogen concentration in *C. angustifolia* shoots was only affected by nitrogen treatment, with nitrogen concentrations in 20% and 60% H_2O treatments typically being similar to one another (F-ratio = 7.9421, 5df, $p < 0.0001$; Figure 5). The 15 mg N kg^{-1} soil, 60% H_2O treatment allowed *C. angustifolia* individuals to sequester the most nitrogen in shoot tissue, averaging 4.9% nitrogen, while plants that received no added nitrogen averaged less than half as much tissue nitrogen. Shoot tissue nitrogen in *L. lasiocarpum* individuals was not different between any treatments under either watering treatment.

S. columbariae was the only species for which both nitrogen and water were significant factors in tissue nitrogen concentration ($p < 0.0001$ for both factors; Figure 5); for all other species, nitrogen was the only treatment that affected tissue nitrogen allocation. Under both 20% and 60% H_2O treatments, 20 mg N kg^{-1} soil had the highest percentage of tissue nitrogen and 0 mg N kg^{-1} soil had the lowest ($p = 0.0123$, 0.0009; respectively).

Tissue nitrogen concentration in *E. cicutarium* was only affected by nitrogen treatment. Within the 20% H_2O treatment, *E. cicutarium* followed its typical pattern with the highest nitrogen concentrations in 20 mg N kg^{-1} soil and decreased to the lowest in 0 mg N kg^{-1} soil in numerical order. However, the analysis of tissue nitrogen concentrations under 60% H_2O elicited the only departure from this pattern, with 15 mg N kg^{-1} soil allowing *E. cicutarium* individuals to store more nitrogen in shoots than any other treatment (F-ratio = 5.9117, 5df, $p = 0.0011$; Figure 5).

The relative growth rate (RGR) of every species varied with the nitrogen and watering treatments, although the differences in growth rates were consistently small. *C. angustifolia* achieved its highest RGR under the 5 mg N kg^{-1} soil, 60% H_2O treatment, which was higher than 0 and 10 mg N kg^{-1} soil, 20% H_2O and also the 2.5 mg N kg^{-1} soil, 60% H_2O treatment ($p = 0.0001$; Figure 6). *L. lasiocarpum* RGR was affected by both nitrogen and watering treatments ($p = 0.0163$ and $p < 0.0001$; respectively; Figure 6). The

60% H_2O treatments elicited fast RGR, as did the 2.5 – 15 mg N kg^{-1} soil treatments. However, the 0 and 20 mg N kg^{-1} soil treatments were not significantly different in RGR.

S. columbariae growth rates were also influenced by both water and nitrogen treatments ($p < 0.0001$ for both factors; Figure 6), with individuals growing in 60% H_2O pots exhibiting faster growth rates than the low watering treatment. *E. cicutarium* demonstrated a similar pattern to the other species, with the high-water treatment increasing growth rate over the 20% H_2O treatment ($p < 0.0001$; Figure 6).

Discussion

Several studies have shown that invasive species are often more nitrophilous than natives (Huenneke et al. 1990, Burke and Grime 1996, Brooks 2003, Daehler 2003, Gross et al. 2005, Schmid et al. 2008), especially in areas that have been artificially enriched by nitrogen deposition. In this study, the invasive annual forb *E. cicutarium* was the only species to consistently garner the advantages of increasing nitrogen fertilization. While *E. cicutarium* was able to increase growth and nutrient allocation with each incremental addition of fertilizer, native annual forbs tended to obtain maximum biomass, size, or flower number at intermediate levels of nitrogen such as 10 or 15 mg N kg^{-1} soil. Due to this enhanced resource uptake ability, *E. cicutarium* continued to increase in shoot biomass, rosette width, and flower number up to 20 mg N kg^{-1} soil. These data support my original hypothesis that *E. cicutarium* would experience the most benefits of nitrogen fertilization and also demonstrate that *E. cicutarium*, unlike native annual desert species, was able to experience the benefits of increasing nitrogen regardless of watering treatment. Previous studies have also found that *E. cicutarium* aboveground biomass production is not strongly affected by water stress (Peláez et al. 1995, Busso et al. 1998) and that the species experiences heightened benefits of increases in water availability due to a lower soil moisture threshold when compared to native annuals (Gutiérrez 1992). Furthermore, Busso et al. (1998) found that reproductive plasticity of *E. cicutarium* allows it to allocate nutrients to fruits in the case of early-season water stress in order to ensure reproductive success.

Biomass allocation for *E. cicutarium*, analyzed as R:S, also demonstrated that *E. cicutarium* had a consistently low R:S compared to native species. Small R:S suggests that *E. cicutarium* repeatedly allocated resources to aboveground biomass at the expense of the roots. However, R:S was not different between nitrogen treatments within the 20% H_2O treatment, which is consistent with a previous study in which root growth of *E. cicutarium* increased under water stress (Busso et al. 1998). The suite of characteristics leading to enhanced shoot growth and low R:S could allow *E. cicutarium* to remain competitive with native species in desert ecosystems, even under drought conditions.

Native R:S also tended to respond negatively to nitrogen fertilization, which is expected because desert annual survival and reproduction is strongly correlated with plant size (Mulroy and Rundel 1977), which leads to decreases in R:S. Therefore, when nutrients are not limiting, native annuals allocate relatively more biomass aboveground than belowground. *C. angustifolia* was the only native species for which the decrease in R:S with increasing nitrogen was significant in both the 20% and 60% H_2O treatments.

This response is interesting because it appears that *C. angustifolia* allocated biomass similarly to *E. cicutarium*, perhaps favoring aboveground reproductive effort in lieu of nutrient acquisition by increasing root biomass under water stress. Neither *L. lasiocarpum* nor *S. columbariae* demonstrated this pattern of allocation under low water. In fact, the decrease in R:S with increasing nitrogen level was not significant for *L. lasiocarpum* under either watering treatment and *S. columbariae* R:S did not differ under any treatment combination. *L. lasiocarpum* tended to have the highest R:S under each treatment combination, which suggests that it uses a different growth strategy than the other species in this study. By maintaining a high R:S, *L. lasiocarpum* does not have to increase root allocation under stressful conditions and is prepared to absorb a pulse of soil resources if one occurs.

The growth responses of both the native annual forbs and the invasive forb *E. cicutarium* also confirmed my hypothesis that the 60% H_2O watering treatment would confer the most benefits regardless of nitrogen treatment, which reinforces the fact that desert annual plants are primarily water limited. Without adequate water availability, native annual forbs were not always able to take advantage of increased soil nitrogen. In another study, Gutiérrez (1992) found that in a very dry year, neither native nor exotic annual species in the desert were capable of responding to fertilizer. Williams and Bell (1981) found that when resource stress is relieved in desert plant communities, it could lead to increased vegetative and reproductive biomass. For the native species in this study, stress was only adequately relieved under the high-water (60%) treatment.

Although shoot biomass allocation depended more on water than nitrogen for most species, shoot tissue nitrogen concentrations tended to significantly increase with increasing nitrogen under both low and high water availability, with the exception of *L. lasiocarpum*. The ability of both native and invasive annual species to take up extra nitrogen in this study is consistent with previous research (Williams and Bell 1981, Yoshida and Allen 2001, Brooks 2003, DeFalco et al. 2003). However, the acquisition of extra nitrogen in aboveground tissue did not always translate into increases in shoot biomass. This is likely due to the fact that nitrogen-poor plants tend to allocate nitrogen to reproduction at the expense of vegetative organs throughout their lifecycles in order to conserve nitrogen for seeds and ensure persistence in future growing seasons (Williams and Bell 1981).

Although significant changes in growth rate were detected for all species, RGR had consistently low variability across all treatment combinations. RGR is an inherent characteristic and species in favorable environments often have higher RGR than species from less favorable environments (Chapin 1980); however, native desert annuals and ruderal weed species often have high RGR because of the need for opportunistic use of temporally favorable growing conditions. In a competition experiment conducted under limiting nutrient supply, relative growth rates were decreased but the inherent ability of one species to grow faster than another was not changed (Lambers and Poorter 1992). The results of this study show similar trends, where species only increased or decreased RGR by a small amount. *E. cicutarium* demonstrated the greatest increase in RGR from

$0.07\ g\ g^{-1}\ day^{-1}$ under low water and low nitrogen conditions to $0.09\ g\ g^{-1}\ day^{-1}$ under the 20 mg N kg^{-1} soil, 60% H_2O treatment, once again demonstrating its apparently limitless ability to make use of increases in soil water and nitrogen.

Ecological implications

The ecological significance of this work lies in the differences between native and invasive annual responses to nitrogen and water. Although this study and a field study (Schneider chapter 4) demonstrated that desert native annual forbs have the ability to respond positively to increases in soil nitrogen, this study also shows that *E. cicutarium* experiences the most consistent benefits. Additionally, it reveals a lack of sensitivity to water stress in *E. cicutarium*, which likely confers a major competitive advantage over native species because natives tend to be conservative in growth as a result of adaptations to a stochastic, resource-limited environment (Chapin 1980, Vitousek 1982). A study related to this one found that invasive annual grasses in the desert may be able to produce biomass beyond the fire threshold for creosote bush scrub communities when water and nitrogen availability are high (Rao et al. 2010), especially in areas affected by nitrogen deposition. Further research is needed to extrapolate these greenhouse results and determine whether or not *E. cicutarium* would be capable of producing enough aboveground biomass to carry fire. However, the implications for increased competitive ability and biomass production are strong.

The lack of flower production or reduced growth in some native annual species under high water and nitrogen treatments suggests that if resource availability increases too much, it may alter phenology by delaying flowering. The number of flowers produced by *C. angustifolia* and *L. lasiocarpum* in pots with no nitrogen added and treated with 20% H_2O was not different from that of plants receiving 20 mg N kg^{-1} soil and 60% H_2O. There was also no difference in flower number between 0 and 20 mg N kg^{-1} soil under the 60% H_2O treatment for *S. columbariae*. *E. cicutarium* is the only species that produced significantly more flowers under high water and nitrogen than pots receiving no nitrogen. Similarly to the species in this study, Mojave Desert winter annuals have also shown variable responses to water and nitrogen treatments (Whitford and Gutiérrez 1989). By delaying allocation to reproduction under high resource availability, native species could become vulnerable to sudden deep soil drying due to the onset of high temperatures or an early end to the winter rainy season (Schwinning and Ehleringer 2001). An even more alarming result of this work is the finding that *E. cicutarium* has the ability to increase growth rate with increases in nitrogen under both high and low watering treatments. Elevated growth rate combined with increased reproductive effort could lead to dominance aboveground as well as belowground in the soil seed bank.

Taken together, the results from this study suggest that, although native species can benefit from increased resources, they experience maximum benefits under high water and intermediate soil nitrogen levels. On the other hand, the invasive annual forb *E. cicutarium* continued to benefit from increased nitrogen even under low water conditions.

Even small inputs of nitrogen can facilitate invasive species success in arid ecosystems (Brooks 2003, Chambers et al. 2007) and parts of the Coachella Valley currently receive up to 9 kg $ha^{-1}yr^{-1}$ of nitrogen deposition (Tonnesen et al. 2007). Under increased urbanization and predicted global climate change scenarios, nitrogen deposition and temperatures will likely increase and the already unreliable precipitation events in the Colorado Desert may become more sporadic (Hayhoe et al. 2004, Weiss and Overpeck 2005). The ability of *E. cicutarium* to resist drought and take advantage of increasing soil nitrogen could lead to increased abundance in the desert. Although native annuals are adapted to desert environments, they are not able to utilize excess soil resources to the same degree as *E. cicutarium*. Conservation and *E. cicutarium* removal efforts should concentrate on areas of high nitrogen deposition and abundant invasives, where native species are likely to encounter higher invasive densities than areas with low nitrogen deposition or where invasive species are relatively less abundant.

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Figure 3.1. Shoot biomass for each species was analyzed by treatment using a two-way ANOVA. Treatments separated by different letters are significantly different using Tukey's HSD ($\alpha = 0.05$). Note that the shoot biomass scale varies with species.

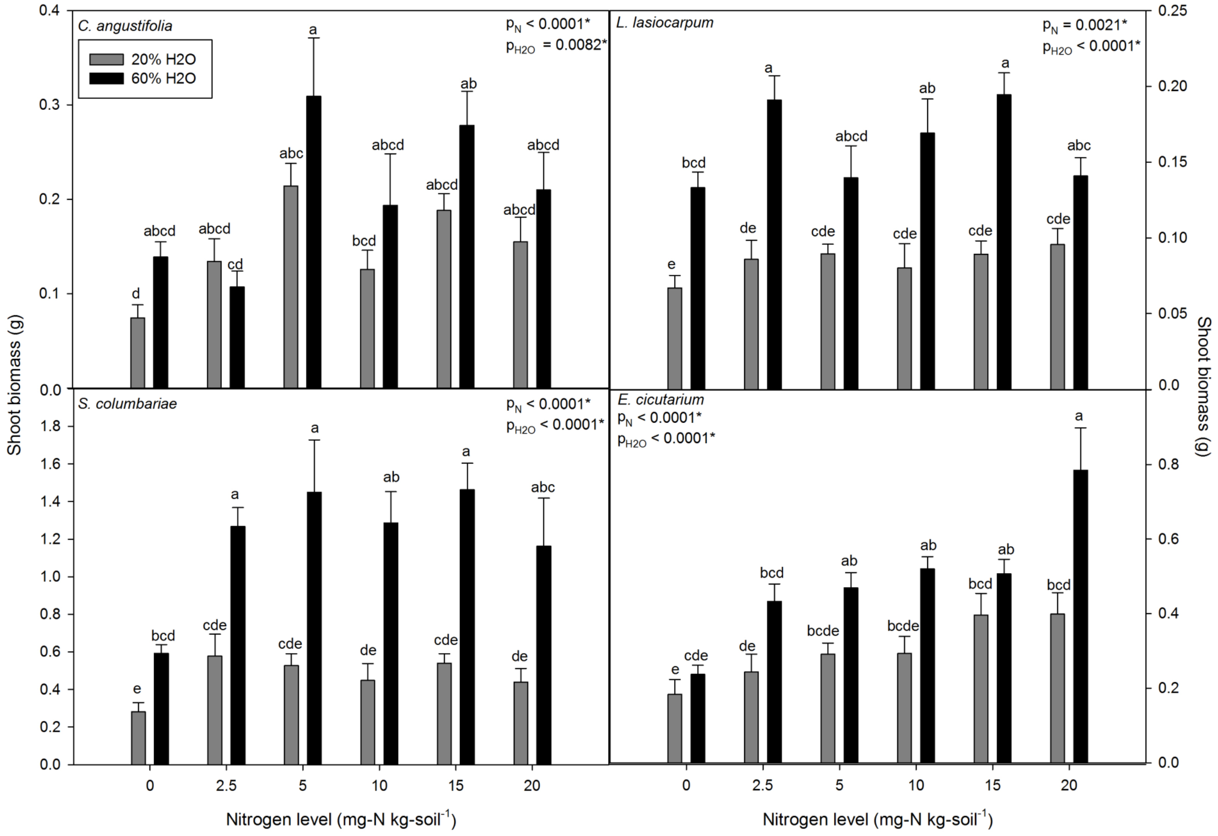


Figure 3.2. Plant height or basal rosette width (depending on species) was analyzed using two-way ANOVA. Treatments separated by different letters are significantly different using Tukey's HSD ($\alpha = 0.05$). Note that the height or rosette width scales vary by species.

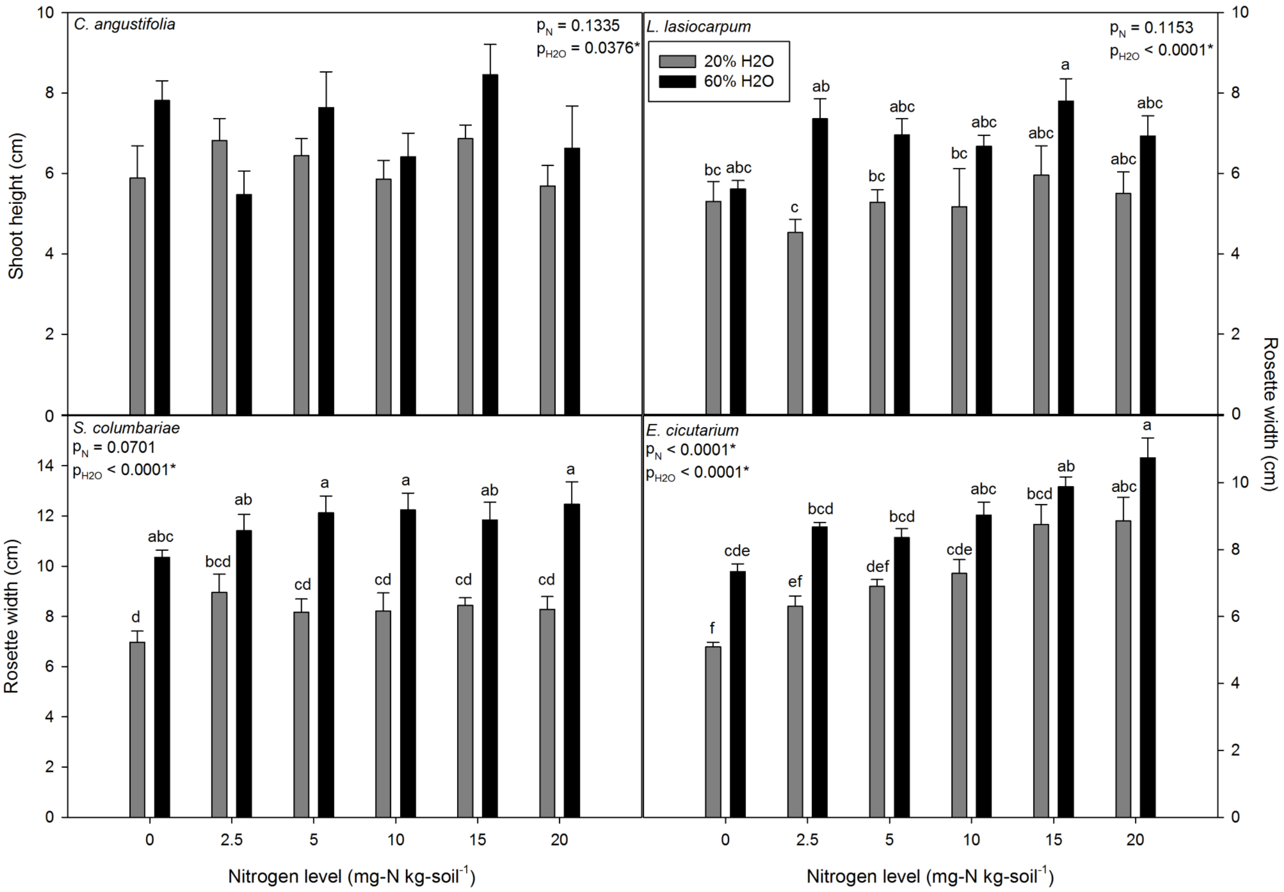


Figure 3.3. Number of flowers was analyzed by nitrogen and watering treatment using a Kruskal-Wallis test or two-way ANOVA. Treatments separated by different letters are significantly different using Tukey's HSD ($\alpha = 0.05$). Note that the scale for number of flowers varies with species.

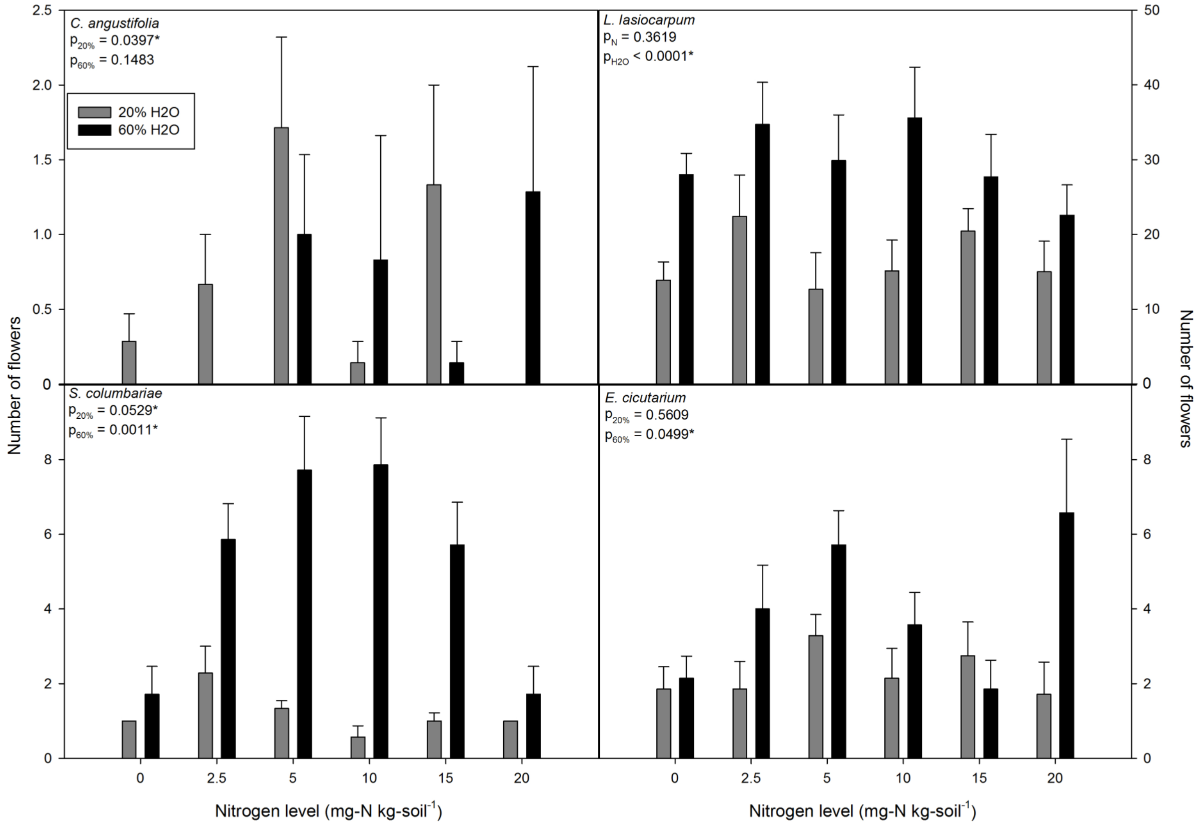


Figure 3.4. Root-to-shoot ratio was analyzed by treatment using a two-way ANOVA. Treatments separated by different letters are significantly different using Tukey's HSD ($\alpha = 0.05$). Note that the root:shoot axis scale varies by species.

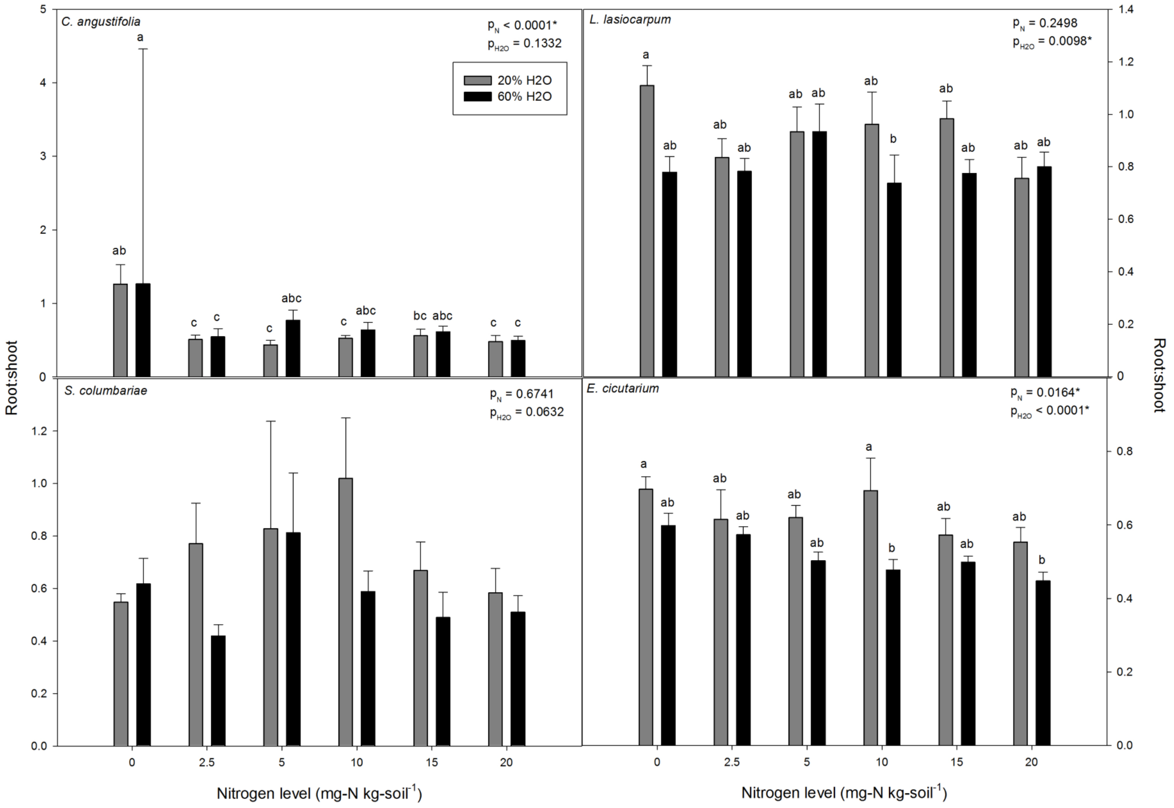


Figure 3.5. Percent tissue nitrogen was analyzed by nitrogen and watering treatment using a Kruskal-Wallis test or two-way ANOVA. Treatments separated by different letters are significantly different using Tukey's HSD ($\alpha = 0.05$). Note that the % tissue nitrogen scale varies by species.

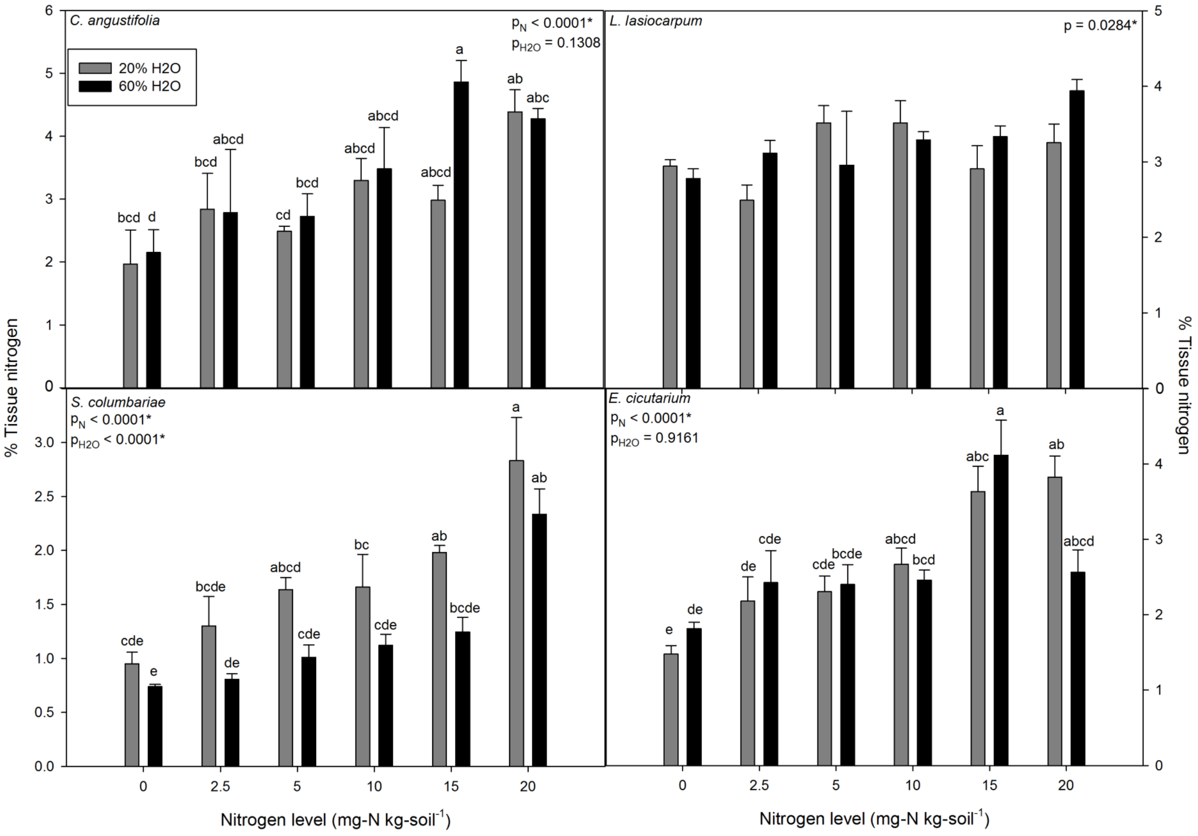
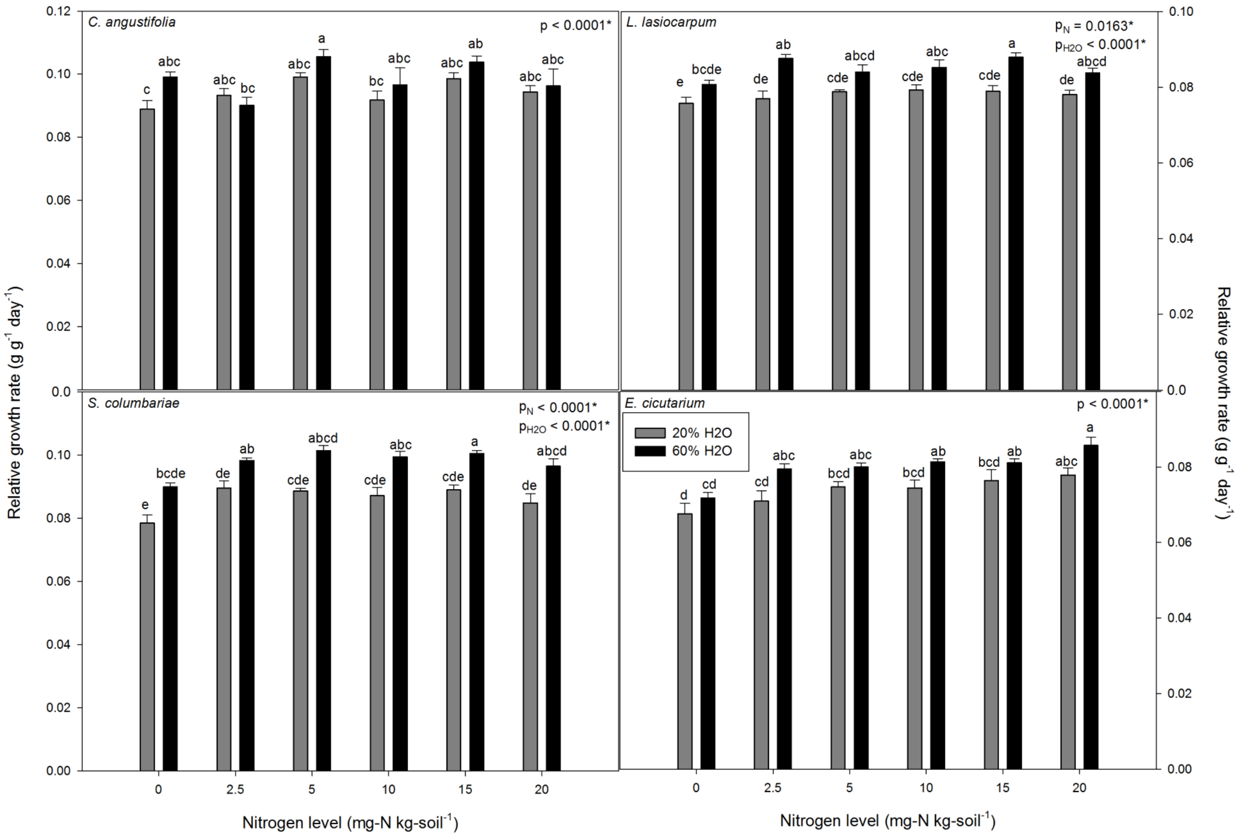


Figure 3.6. Relative growth rate (g g^{-1} day^{-1}) was analyzed by treatment using a two-way ANOVA or Kruskal Wallis test, depending on the normality of the data. Treatments separated by different letters are significantly different using Tukey's HSD ($\alpha = 0.05$). Note that the scale of the GR axis varies by species.



Chapter 4. Effects of nitrogen fertilization and exotic invasive removal on native annual forbs in the Colorado Desert

Abstract

Anthropogenic nitrogen deposition and exotic invasive species threaten desert plant communities. Soil nitrogen pulses can increase competition in low nutrient systems such as creosote bush scrub communities in the Colorado Desert. In this study, I tested the hypothesis that both native and invasive winter annuals can exploit increased soil nitrogen and that natives experience the greatest benefit when exotic invasive plants are removed. Treatments consisted of four combinations of nitrogen fertilization (control and 25 kg N ha^{-1} as NH_4NO_3) and exotic invasive removal (control and Fusilade II® plus hand weeding). Both natives and invasives responded positively to nitrogen fertilization, but plant responses were typically specific to the site and season in which responses were evaluated. Both native and invasive plant productivity were consistently increased by nitrogen additions, although percent cover and density responses were variable. Soil extractable nitrogen and exotic invasive removal had cumulative effects, which resulted in measurable increases in NH_4^+ and NO_3^- in fertilized plots and a decrease in invasive density in exotic invasive removal plots over time. I also compared soil and vegetation in fertilized plots to that found along shrub driplines to determine whether nitrogen fertilization alone can imitate the benefits of the fertile island effect. My results showed

that percent cover, tissue C:N, and plant productivity were not significantly different between fertilized and shrub understory plots, despite more than five-fold higher extractable soil nitrogen in fertilized plots. Since species composition can vary between the interspace and shrub understories, the ability of nitrogen fertilization to mimic the shrub understory could lead to changes in the species composition of intershrub spaces. This research highlights the ability of native annuals to take advantage of additional soil nitrogen in the field, even in the presence of invasives. It also demonstrates that nitrogen fertilization can simulate the fertile island effect in intershrub spaces, both of which have important implications for conservation and restoration of desert plant communities.

Introduction

Exotic invasive species have the ability to degrade ecosystems (Elton 1958, Simberloff 1996, Mack et al. 2000), and California's flora has an exceptionally high proportion of invaders. Many of the first major introductions of exotic plants into California occurred with the arrival of Spanish expeditions in 1769 (Parish 1920), leading to invasions in developed areas along the coast and in agricultural fields. These invasions caused long-term ecosystem disruption and even vegetation-type conversion of plant communities such as coastal sage scrub, woodlands, and grasslands that are dominated by exotic invasives across much of their ranges (D'Antonio and Vitousek 1992, Minnich and Dezzani 1998, Stylinski and Allen 1999, Alvarez and Cushman 2002, Minnich 2008).

Although California's deserts have been historically less invaded than coastal areas, anthropogenic influences such as agriculture, urbanization, and their resulting impacts have allowed invasive species to become permanent residents. Through the burning of fossil fuels and proliferation of industrial fertilizers, human beings have doubled the amount of terrestrially available nitrogen on the earth's surface (Vitousek et al. 1997) and as agriculture and urbanization have spread inland, nitrogen deposition has altered California's desert ecosystems. Nitrogen deposition has been shown to have serious long-term consequences at the ecosystem scale and can result in decreases in species diversity, altered competitive interactions, and shifts in species composition and dominance (Vitousek et al. 1997, Bobbink et al. 1998, Clark and Tilman 2008, Rao and Allen 2010).

The combination of a harsh climate and relatively nutrient poor soils in the desert were thought to be a barrier for most invasive species; however, increased soil nutrients due to nitrogen deposition have allowed exotic invaders to successfully establish and spread (Brooks 1999b, 2003). To the west, the Los Angeles air basin receives levels of nitrogen deposition that can exceed 30 $kgha^{-1}yr^{-1}$ (Fenn et al. 2003) and although the desert currently experiences much lower rates of nitrogen deposition, urban sprawl threatens to increase deposition in the future. If nitrogen deposition loads continue to increase and spread farther inland, they could exacerbate the problem of invasive species spread and further alter soil nutrient cycling.

Exotic invasive success is the result of complex interactions between the abiotic environment (Milbau et al. 2003, Suding et al. 2004, Dimitrakopoulos et al. 2005), the traits of the invasive species (Rejmanek and Richardson 1996, Brooks 1999b, Milbau et al. 2003), and the traits of native species in the community (Mack et al. 2000, Smith et al. 2004, Gilbert and Lechowicz 2005). Invasive annual invaders often have a rapid phenology that allows them to take advantage of light, soil moisture, and nutrients before native annuals are present aboveground (Baker 1974, DeFalco et al. 2007, Marushia 2009) and the affinity of exotic invaders for increased soil nitrogen in the desert is well documented (Brooks 2003, DeFalco et al. 2003, Allen et al. 2009, Rao and Allen 2009, Rao and Allen 2010). Some of the most common exotic invasive species in the Colorado Desert, and the invasive species of interest in this study, are *Schismus barbatus*, *S. arabicus*, *Erodium cicutarium*, and *Brassica tournefortii*. *S. barbatus* and *S. arabicus* frequently co-occur and are very similar in morphology, and are treated together as *Schismus* in this paper. *Schismus* spp. (Mediterranean split grass) are invasive annual grasses native to the Mediterranean region (Brooks 2000c, a) and arrived in California in the middle of the 20th century (Minnich and Dezzani 1998, Brooks 2000c). *Schismus* is capable of competing for soil nutrients with native annual plants and responds positively to increased soil nitrogen (Brooks 2003, Allen et al. 2009, Rao and Allen 2010). *Schismus* also exhibits semi-conservative seed germination and may use short-term seed banking, a strategy usually employed by natives to prevent germination during unfavorable conditions (Brooks 2000c).

E. cicutarium (filaree) is an invasive annual forb native to Mediterranean Europe (Minnich and Dezzani 1998). It likely arrived prior to Spanish settlement and spread throughout California by the 1800s (Mensing and Byrne 1998, Minnich 2008). *E.*

cicutarium has the advantage of rapid phenology and high seed output, but its hard impermeable seed coat and staggered germination allow it to create a long-term persistent seed bank, giving it a competitive edge over other invasive species and the ability to avoid drought by remaining belowground during unfavorable growing seasons (Harper 1977, Roberts 1981, Mayor et al. 1999).

B. tournefortii (Sahara mustard) is an invasive annual forb native to the deserts of Northern Africa and the Middle East (Sanders and Minnich 2000). It arrived in California as a date palm contaminant in the early 1900s and spread to the Coachella Valley by 1927 (Sanders and Minnich 2000). *B. tournefortii* is larger, hardier, and more likely to reproduce than native annuals under both wet and dry conditions, making it a formidable competitor (Marushia 2009). One study found that the presence of *B. tournefortii* reduced flower and seed production of native annuals by 80-90%, leading to a higher proportion of *B. tournefortii* in the soil seed bank (Barrows et al. 2009). Although it was present, *B. tournefortii* was better represented under shrubs than in the interspace at these sites and was not a major competitor within the study plots.

In addition to the direct competitive effects of exotic invaders, they can also alter ecosystem processes such as fire regimes. In high-density years, exotic invasive biomass can create fuel connections between otherwise widely spaced shrubs. This biomass, especially grasses, disarticulates more slowly than most native annuals, creating a fine layer of persistent fuel between shrubs that can increase fire risk and intensity

(Brooks 1999a, Sanders and Minnich 2000, Rao and Allen 2010). The combined effects of nitrogen deposition and exotic invasion create a positive feedback on fire frequency that often favors invasive species.

This study sought to determine how nitrogen deposition affects the competitive interaction between native and invasive annual species, as well as how native annuals are affected by increased nitrogen when exotic invasive annuals are removed in the Colorado Desert. It is generally assumed that native annuals suffer reductions in density, percent cover, and diversity under the effects of nitrogen deposition and invasive annuals. However, it is unknown how native annual species will respond to increases in nitrogen when exotic invasives are removed. My hypotheses were that exotic annual species have a competitive effect on native annuals and that natives would benefit from exotic invasive removal. I expected both native and invasive species to benefit from nitrogen additions, but that the benefit to invasives would be greater than to natives. I also anticipated that native annual species would experience the largest benefits from increased soil nitrogen in plots where invasive species were removed.

A secondary objective of this study was to compare the effects of nitrogen fertilization in the intershrub spaces to the “fertile island effect” (Garcia-Moya and McKell 1970) created around shrubs in the desert. In low-desert communities such as creosote bush scrub (*Larrea tridentata*), the areas beneath and surrounding shrubs offer shade, increased soil moisture, and elevated soil nutrient levels, creating a more hospitable environment for annual plants (Garcia-Moya and McKell 1970, Garner and

Steinberger 1989). I sought to determine whether increased soil nitrogen alone could simulate conditions similar to the fertile island effect, leading to increases in plant productivity. I hypothesized that the effects of fertilizer on interspace vegetation would mimic the fertile island effect, although benefits may be slightly weaker due to differences in shade and moisture availability.

Methods

Study sites

Two field sites located near Desert Hot Springs in the Coachella Valley of Southern California were used in this study. The Coachella Valley is flanked by the San Jacinto and Santa Rosa Mountains to the west, by the Little San Bernardino Mountains to the north and east, and the Salton Sea to the south. The valley is in the northwestern Colorado Desert, a subdivision of the Sonoran Desert. Average rainfall at the nearby Palm Springs weather station is approximately 140mm per year, based on historical data from 1927 – 2005 (Western 2010).

Site 1 (33°53’30.687”, 116°27’45.169”) is dominated by creosote bush scrub (*Larrea tridentata*) vegetation, with an ephemeral community of winter annual plants filling in the intershrub spaces during the rainy season. The elevation of Site 1 is 219m. The soil is Myoma fine sand, which is rapidly permeable, moderately alkaline (pH approx. 8.2), and has an available water capacity from 8.9 – 14 cm (Knecht 1980).

Site 2 (33°52’49.812”, 116°28’46.115”) is approximately 2km southwest of Site 1 and has the same vegetation type as Site 1. The elevation of this site is 195m and the soil type is Carsitas gravelly sand. This soil type is characterized by gravelly sand with an available water capacity down to 5 – 10.18 cm. These soils are excessively drained with little runoff and are moderately alkaline (pH approx. 8.4) (Knecht 1980). Nitrogen deposition at both sites was estimated to be approximately 9.67 kg N ha^{-1} yr^{-1} using a deposition model (Tonnesen et al. 2003).

Experimental design

Sites 1 and 2 were set up identically using a randomized block design. Each site contained 12 blocks made up of four plots each. Blocks were 5x5 m^2 and the plots within each block were 1x1 m^2. Four treatments were implemented in this study in a 2x2 factorial arrangement with two levels or fertilizer and two levels of weed removal. A buffer zone was implemented between plots to prevent non-target herbicide effects and fertilizer drift (Figure 4.1). Plots received a fertilizer treatment of either control with no nitrogen added (NC) or nitrogen-fertilized with 25 kg N ha^{-1} as NH_4NO_3 (NF). Although 25 kg ha^{-1} of nitrogen exceeds the nitrogen deposition levels currently occurring in the Coachella Valley, it is similar to values measured in coastal sage scrub communities near Los Angeles and represents a hypothetical increase in deposition due to increasing urbanization and land use change.

The removal treatments consisted of either invasive annual removal using a combination of herbicide and hand weeding (IR) or control where no invasives were removed (IC). The post-emergence grass-specific herbicide Fusilade II® (Syngenta, Greensboro, North Carolina) was mixed with the surfactant Herbicide Helper® (Monterey Lawn and Garden Products, Inc, Fresno, CA) and applied early in the growing season before most native annuals were present aboveground. One to two weeks after herbicide application, remaining exotic invasive annual forbs were removed from plots using hand weeding. Treatments varied between 2008 and 2009, but were consistent in 2009 and 2010 (see below). Plots relied on natural rainfall and after treatment application no further manipulations were done until the time of data collection and biomass harvest.

At peak season, defined as maximum plant biomass at flowering, aboveground vegetation data (percent cover, species richness, and density) were recorded from the southern half (0.5 m^2) of each of the four plots within the block. The northern half of each plot was divided in half again to create two 0.25 m^2 plots from which destructive measurements (soil samples and aboveground biomass) were collected over consecutive years. Soil samples were analyzed for extractable nitrogen content (NH_4^+ and NO_3^-) to compare how nitrogen fertilization and invasive removal affected plant-available soil nitrogen levels. Aboveground biomass was oven-dried and weighed to create percent cover – biomass regressions to estimate plot productivity. Plant tissue was ground and analyzed for total tissue carbon and nitrogen in order to determine how the experimental treatments affected plant tissue nutrient content.

Site 1 was used in 2008, 2009, and 2010, while Site 2 was used in 2009 and 2010 only. This experiment was set up at Site 1 in the summer of 2007 in order to study the effects of nitrogen deposition and invasive annual grass competition on native annual forbs. The study was preceded by two years of drought (Figure 4.2) leading to little or no germination of winter annuals, but Site 1 had been invaded by exotic grass in previous years. However, 2008 yielded extremely low densities of invasive grass and invasive forbs became more abundant than in prior years. In order to accommodate the change in the invasive community, the treatments were altered to test the effects of both invasive grasses and forbs on native annual forbs. In 2009, a paired site (Site 2) where *Erodium cicutarium* had previously been abundant was added to the study. The treatments at both sites were altered to test the effects of both invasive grasses and forbs on native annuals in order to accommodate the change in the invasive community.

2008 field methods

Field plots were set up at Site 1 in the fall of 2007. Ammonium nitrate fertilizer (NH_4NO_3) was applied in pellet form on December 13, 2007, at the onset of the winter rains. Fusilade II® was applied on January 9, 2008 when annual seedlings were first emerging from the soil. Fusilade II® was mixed according to label rates and applied by hand with a hand-held sprayer. The herbicide application was timed in order to target invasive grasses, which tend to germinate earlier and have a more rapid phenology than native annuals (Baker 1974, Brooks 2000c, Smilauerova and Smilaur 2010). At the time of spraying, the majority of seedlings present were invasive annuals. Some early germinating native annual forbs were present aboveground, however, no native grasses have been found at this site. During the second week of March, aboveground percent cover, density, and species richness were measured in each plot. Aboveground biomass was harvested from each treatment level to create regressions of cover with biomass.

2009 & 2010 field methods

Field plots were set up at Site 2 in the fall of 2008. Ammonium nitrate fertilizer (NH_4NO_3) was applied in pellet form on December 15, 2008 and December 11, 2009 at both Site 1 and Site 2. Fusilade II® was applied on January 9, 2009 and January 12, 2010 using a hand-held sprayer. At the time of spraying, the majority of seedlings present were exotic invasive annuals; no native grasses have been found at Site 2. On January 26, 2009, all remaining invasives were removed from IR plots using hand weeding at both sites. The primary invasive forb removed was *Erodium cicutarium*, however *Brassica tournefortii* did occur in some plots at Site 1 and was removed. The timing of the winter rains was delayed in the 2009 – 2010 growing season and hand weeding did not occur until February 15, 2010.

During the second and third weeks of March in both 2009 and 2010, aboveground percent cover, density, and species richness were measured in each plot. The 2009 growing season yielded unusually short-statured individuals and low levels of plant biomass, preventing biomass harvesting at peak season. Aboveground biomass was harvested from each treatment level in 2010 to create biomass regressions and determine tissue nitrogen and carbon content. The combination of herbicide application and hand weeding successfully reduced invasive percent cover to 0 – 5%; therefore no invasive biomass was harvested from IR plots in 2010. Soil cores were collected from each treatment to quantify soil extractable nitrogen (NH_4^+ and NO_3^-).

Fertile island experiment

In 2010, vegetation was measured along the dripline of *Larrea tridentata* shrubs at Site 2 in order to compare the effect of nitrogen fertilizer in the intershrub spaces to the natural fertile island effect that occurs beneath and surrounding shrubs in the desert (Garcia-Moya and McKell 1970, Garner and Steinberger 1989). Site 2 is subject to occasional high winds, so measurements were recorded on the leeward side of shrubs, where the majority of understory vegetation occurred. Percent cover, density, and species richness were measured using the same methods as the fertilization study. Aboveground biomass was harvested to create biomass regressions in order to estimate plot productivity and measure total plant tissue carbon and nitrogen. Soil samples were collected to measure soil extractable nitrogen and these values were compared to experimental plots that received nitrogen fertilizer but not invasive removal (NF, IC) and to control plots (NC,IC) to determine whether nitrogen fertilization could simulate the benefits of fertile islands in the intershrub spaces.

The understories of shrubs at Site 1 were heavily invaded by *Brassica tournefortii* and were not suitable for comparison with interspace vegetation, which is relatively devoid of *B. tournefortii*. Therefore, the fertile island study was only conducted at Site 2.

Soil and plant tissue analyses

Total soil and aboveground plant tissue carbon and nitrogen content were determined using a Thermo-Finnigan Flash A1112 soil combustion N/C analyzer system at the University of California, Riverside. Site 1 soils averaged 0.005% nitrogen and 0.072% carbon. Site 2 soils were 0.002% nitrogen and 0.057% carbon. Soil extractable nitrogen was measured using a flow-injection analyzer at the University of California Division of Agriculture and Natural Resources Laboratory (danranlab.ucdavis.edu). Soil nitrate (NO_3^-) and ammonium (NH_4^+) were analyzed separately to determine not only how fertilization and invasive removal affected total available nitrogen, but also whether the two forms of available nitrogen were affected differently.

Data analysis

Vegetation data were grouped and analyzed functionally as either invasive or native, except in 2008. In 2008, invasive annual grass was the only functional group targeted for removal and was analyzed separately from invasive forbs. In 2009 and 2010, invasive grasses and forbs were analyzed together as “invasives.” Tissue carbon-nitrogen ratios (C:N) were calculated using total carbon and nitrogen values. High C:N indicate a higher allocation to carbon in the tissue and is considered to be lower quality litter than tissue that is high in nitrogen content and has a low C:N. Percent cover, density, species richness, productivity, and extractable soil nitrogen were analyzed using one or two-way ANOVA when data were normally distributed or were amenable to transformation. Data that were non-normal and resisted transformation were analyzed using a Kruskal-Wallis test for nonparametric data. All graphs and charts report untransformed data. Significant differences were determined using Tukey's Honestly Significant Difference ($p < 0.05$). All analyses were performed using JMP® statistical software (JMP, Version 8).

Plant density was used to calculate the Shannon-Wiener Index and Pielou's Evenness for each treatment in all years. The Shannon-Wiener Diversity Index was used to calculate the degree of uncertainty in determining the identity of a random individual from the community. The index was calculated as $H' = -\sum(p_i \ln(p_i))$, where p_i represents the proportion of the N individuals in the community that are species i. High H' values reflect high diversity and, therefore, high uncertainty in predicting the identity of a species chosen at random. Pielou's Evenness was calculated using the value derived from the Shannon-Wiener Index as $J' = H'/H_{max}$, where H_{max} is ln(S) and S is species richness. J' values range from zero to one, with values close to one having less variation in species and reflecting high species evenness.

Dry biomass weight and percent cover values were used to create regressions in order to calculate plot productivity. In 2009, low annual plant production prevented accurate biomass harvesting. Therefore, there are no productivity or tissue carbon and nitrogen data for 2009 at either site.

Results

2008 – Site 1

Twenty-four species, including three invasive and 19 native species, germinated in 2008 (Table 4.1). Both percent cover and density of exotic invasive grass were significantly reduced by Fusilade II® application and positively influenced by nitrogen fertilization ($H = 38.67$, 3df, $p < 0.0001$; $H = 37.68$, 3df, $p < 0.0001$), although invasive grass cover was uniformly low across all treatments (Figure 4.3; Figure 4.4). Neither invasive forb cover nor density was affected by invasive grass removal or nitrogen fertilization ($H = 2.08$, 3df, $p = 0.5556$; $H = 0.82$, 3df, $p = 0.844$). This result is likely due to high variability in invasive forb cover across all treatments. Even though native forb cover was not affected by either invasive grass removal or nitrogen fertilization ($H = 0.9624$, 3df, $p = 0.8103$), native forb density was significantly higher in NC than NF plots, especially when invasive grass was not removed ($H = 12.28$, 3df, $p = 0.0065$). Species richness in 2008 was not affected by either treatment and a two-way ANOVA revealed no interaction between invasive grass removal and nitrogen fertilization (F-ratio

= 0.76, 3df, $p = 0.523$; Table 4.2). Shannon-Wiener Diversity indices were low for all treatments, although somewhat higher in Site 1 than Site 2. Pielou's Evenness values were consistently close to one, which is representative of even species distribution (Table 4.3).

Despite increases in invasive grass due to nitrogen fertilization in 2008, total invasive productivity (grass plus forb) was not affected by either treatment (H = 2.32, 3df, $p = 0.5079$). Invasive productivity ranged from 0.7 to 1.7 kg m^{-2} (Table 4.4). Native productivity was also unaffected by the treatments, ranging from 2 to 4.1 kg m^{-2} (H= 4.26, 3df, $p = 0.2347$; Table 4.4).

Tissue nitrogen concentration was evaluated by functional group and showed that invasive grass tissue nitrogen was not affected by fertilization in 2008 (Table 4.5). Invasive forb tissue was influenced by both invasive removal ($p = 0.0301$) and the interaction between invasive removal and nitrogen ($p = 0.0176$; Table 4.5). Invasive forb tissue nitrogen was highest in NC,IC plots with 1.4% tissue nitrogen and lowest in NC,IR plots. Surprisingly, native forb tissue nitrogen was also highest in IC plots.

Given that no exotic invasive grass biomass was harvested from IR plots, a one-way ANOVA was used to analyze treatment effects on grass tissue C:N. Surprisingly, no effect of nitrogen fertilization was detected in invasive grass tissue C:N (F-ratio = 0.27, 1df, $p = 0.6140$; Table 4.5). Invasive forb biomass had a significantly higher leaf tissue C:N when no nitrogen was added and invasive grasses were removed from plots (14.99; F-ratio = 3.62, 3df, $p = 0.0262$; Table 4.5). Although nitrogen treatment was not significant, invasive grass removal and the interaction between grass removal and nitrogen were significant. Only invasive grass removal significantly affected native forb C:N, with the highest C:N being in NC,IR plots (20.21; F-ratio = 5.58, 3df, $p = 0.0019$; Table 4.5).

In order to investigate aboveground nitrogen partitioning, tissue nitrogen concentrations were calculated as kilograms of aboveground nitrogen per hectare. No differences were detected between treatments within functional groups due to nitrogen fertilization (Table 4.4). When partitioning of nitrogen was compared between invasive and native functional groups, native biomass harbored significantly more nitrogen for all treatments except NC,IR in 2008. Native plant tissues accounted for 75 – 85% of aboveground nitrogen in NC,IC, NF,IR, and NF,IC plots. Total aboveground tissue–stored nitrogen ranged from 3.5 – 4.7 kg ha^{-1}.

Total extractable nitrogen was affected by both nitrogen fertilization and invasive plant removal in 2008. Soil nitrogen was lowest in NC,IC plots, but was higher in NC,IC plots; furthermore, NF,IC plots also had higher total extractable nitrogen than NF,IR plots ($p = 0.0833$). Although an analysis of regression did not show significant treatment effects here, a Tukey's HSD separated each group as being significantly different from the others. Soil nitrogen ranged from 8.3 – 25.3 μg/g with NC,IC and NF,IC plots representing the lowest and highest nitrogen concentrations, respectively (Table 4.6a).

2009 – Site 1

In 2009, the exotic invasive grass removal treatment was altered to include removal of all exotic invasive annual species. Results are reported by functional group for either invasive or native species. Nitrogen fertilization treatments were consistent throughout the study.

In 2009, one new native species, *Stephanomeria exigua*, germinated at Site 1 (Table 4.1). The combination of Fusilade II® and hand weeding significantly reduced the cover of invasive species ($H = 35.88$, 3df, $p < 0.0001$; Figure 4.5a.) and nitrogen fertilization significantly increased invasive percent cover from 7.4% in control plots to 19.5% in fertilized plots. Native percent cover was also significantly increased by nitrogen, especially in invasive removal plots (44.8%; $H = 17.63$, 3df, $p = 0.0005$; Figure 4.5a.).

Similar to percent cover, invasive plant density was significantly reduced by removal treatments, however, there was no difference due to nitrogen ($H = 36.5$, 3df, $p < 0.0001$). Average invasive density was lower than native density for all treatments, achieving a maximum average density of only 107 plants m^{-2} in NC,IC treatments. Native forb density was significantly higher in NC plots, regardless of whether or not invasives were removed ($H = 18.23$, 3df, $p = 0.0004$; Figure 4.6a), with maximum density reaching over 600 plants per m^2 in NC,IC plots. Only exotic invasive removal affected species richness, with more species represented in plots where invasives were present (F-ratio = 3.57, 3df, $p = 0.0215$; Table 4.2).

In 2009, total soil extractable nitrogen was only separated by nitrogen treatment. Soil nitrogen was higher in fertilized plots versus unfertilized plots ($p = 0.0001$), with fertilized plots containing nearly five times as much nitrogen as unfertilized plots (Table 4.6a). Unlike in 2008, invasive plant removal did not significantly affect soil nitrogen concentrations.

2009 – Site 2

Site 2 had lower species richness than Site 1, with only 20 species germinating within the study plots (Table 4.1). However, as at Site 1, exotic invasive percent cover and density were significantly reduced by the invasive removal treatments ($H = 30.98$, 3df, $p < 0.0001$; $H = 37.79$, 3df, $p < 0.0001$; Figure 4.7a). Total native cover was normally distributed and a two-way ANOVA determined that both nitrogen fertilization and invasive removal had significant effects, but the interaction between the two treatments was not significant (F-ratio = 5.6, 3df, $p = 0.0024$; Figure 4.7a). Native cover was highest in NF,IR plots (39.9%) and lowest in NC,IC plots (17.2%).

Unlike Site 1, invasive density at Site 2 was higher than native density in IC plots. Invasive density was significantly reduced in IR plots and there was no difference between nitrogen treatments ($H = 37.8$, 3df, $p < 0.0001$; Figure 4.8a). Native density was not different. A two-way ANOVA test found that species richness was not significantly affected by nitrogen or invasive treatments (F-ratio = 2.13, 3df, 0.1095; Table 4.2), however, Tukey's HSD separated groups based on nitrogen treatment.

Total extractable soil nitrogen was lowest in unfertilized plots and peaked at 33 µg/g in NF,IR plots ($p = 0.0001$). NF,IC plots were not significantly different from NF,IR plots or either of the NC plots. The lowest levels of soil nitrogen were measured in NC,IC plots (5.6 µg/g; Table 4.6b).

2010 – Site 1

The relatively high rainfall in 2010 led to the germination of 30 species at Site 1, six more species than in the first year of the study (Table 4.1). Total exotic invasive cover was significantly higher in nitrogen-fertilized plots than under any other treatment (15.25%; $H = 33.84$, 3df, $p < 0.0001$; Figure 4.5b), but invasive density was only affected by the invasive removal treatment ($H = 37.17$, 3df, $p < 0.0001$; Figure 4.6b). Fusilade II® and hand weeding were successful at reducing invasive cover and density, reducing them to almost zero. Native percent cover was positively influenced by nitrogen fertilization ($H = 8.84$, 3df, $p = 0.0315$), but native density was not significantly different under any treatment combination ($H = 5.36$, 3df, $p = 0.147$). Only invasive removal influenced species richness values, with the highest richness in NC,IC plots (12.4; F-ratio = 3.08, 3df, $p = 0.037$; Table 4.2).

Exotic invasive plant productivity was low in all plots, but NF,IC plots were significantly more productive than all other treatment combinations ($H = 42.01$, 3df, $p < 0.0001$; Table 4.4). Native species were more productive than invasives under all treatment combinations, but only NF,IR plots were significantly more productive than all others ($H = 25.0$, 3df, $p < 0.0001$; Table 4.4). Invasive plant tissue nitrogen was higher in fertilized plots than unfertilized ($p = 0.0001$), as was native tissue nitrogen ($p = 0.0165$; Table 4.5). Similar to 2008, native annual forb tissue nitrogen was highest in NF,IC plots, although invasive removal was not a significant factor. Furthermore, native tissue nitrogen concentration was roughly twice as high in 2010 compared to 2008, likely due to increased precipitation in 2010.

As expected, invasive C:N was higher in unfertilized plots versus NF plots ($H = 10.5$, 1df, $p = 0.0012$; Table 4.5). Exotic invasive removal did not affect native C:N, but unfertilized plots had higher C:N than fertilized plots (F-ratio = 3.34, 3df, $p = 0.0368$).

Unlike in 2008, aboveground nitrogen partitioning was different within functional groups in 2010 (Table 4.4). For native species, tissue nitrogen concentration was highest in NF,IR plots and lowest in NC,IC plots (6.5 and 1.7 kgha^{-1}, respectively; $p < 0.0001$). Invasive species stored more aboveground nitrogen in fertilized plots than control plots, which were not different from zero (3.0 and 0.63 kgha^{-1}, respectively; $p < 0.0001$). Within treatments, aboveground nitrogen was always higher in native versus invasive species. In NF,IR plots, natives were able to acquire almost as much nitrogen as invasive and native plants combined in NF,IC plots (6.5 and 7.4 kgha^{-1}, respectively).

As in 2009, total soil extractable nitrogen was only affected by nitrogen fertilization. Soils from NF plots contained up to 20 times more nitrogen than NC plots ($p = 0.0001$; Table 4.6a), with the highest values measured in NF,IC plots (64.8 μg/g).

2010 – Site 2

Despite the high rainfall in the 2010 growing season, only 18 species germinated at Site 2 (Table 4.1). However, as in all other years, the invasive removal treatments were successful at reducing or eliminating exotic invasive plants from IR plots. Invasive plants in NF plots had significantly higher percent cover than NC plots and IR plots, regardless of nitrogen treatment ($H = 39.93$, 3df, $p < 0.0001$; Figure 4.7b). However, invasive density was only affected by invasive removal and not by nitrogen treatment ($H = 38.99$, 3df, $p < 0.0001$; Figure 4.8b). A two-way ANOVA did not find any significant differences in percent cover of native annual forbs (F-ratio = 1.6, 3df, $p = 0.2036$), but a Tukey's HSD distinguished natives in NF,IR plots as having significantly higher cover than those in NC,IC plots(Figure 4.7b). Nitrogen and invasive removal treatments had no effect on native density, despite large differences between NF,IR and NF,IC plots. NF,IR plots had very high standard error, which likely overshadowed any significant effects of fertilization or invasive removal ($H = 4.6749$, 3df, $p = 0.1972$; Figure 4.8b).

Species richness was significantly higher in NC,IC plots than any other treatment (F-ratio = 5.1268, 3df, $p = 0.004$; Table 4.2). A two-way ANOVA determined that nitrogen and invasive treatments were significant, but the interaction between them was not (F-ratio = 8.11, 1df, $p = 0.0066$; F-ratio = 7.2, 1df, $p = 0.0102$). Invasive plant productivity was five times higher in NF plots than NC plots ($H = 44.79$, 3df, $p < 0.0001$; Table 4.4). Native productivity was only significantly affected by nitrogen fertilization, which increased productivity to 3.8 kg m^{-2} under the NF,IR treatment from 0.7 kg m^{-2} in the NC,IC treatment ($H = 26.6$, 3df, $p < 0.0001$; Table 4.4).

Exotic invasive plant tissue nitrogen was not affected by nitrogen fertilization ($p = 1099$; Table 4.5). However, both nitrogen and invasive removal treatments significantly affected native forb tissue nitrogen, as well as the interaction of the two ($p = < 0.0001$; $p = 0.005$; $p = 0.0215$; Table 4.5). Native annual forb tissue nitrogen was elevated in nitrogen fertilized plots and highest in NF,IR plots (2.9%), suggesting that there was competition with invasives for soil nitrogen.

Analysis of tissue C:N did not show any changes in nutrient content for invasive species due to nitrogen fertilization ($H = 2.82$, 1df, $p = 0.0929$; Table 4.5), however native annual forb tissue was affected by both nitrogen and invasive treatments. As expected, native C:N ratios were highest in unfertilized plots and the lowest in NF,IR plots (F-ratio = 22.15, 3df, $p < 0.0001$; Table 4.5). Tissue C:N was also analyzed to compare native and invasive plant tissue nutrient content within years, with 2008 being the only year where invasive and native C:N were significantly different (data not shown).

Tissue nitrogen was used to determine how aboveground nitrogen was partitioned across treatments and between functional groups (Table 4.4). Invasive plants had the highest tissue nitrogen concentrations in fertilized versus unfertilized plots, which were not significantly different from IR plots ($p < 0.0001$). Native tissue nitrogen was highest in NF,IR, followed by NF,IC plots (3.8 kg ha^{-1}, 2.0 kg ha^{-1}, respectively) and NC plots were not different from one another ($p < 0.0001$).

In 2010, both NF plots were distinct from NC plots and contained up to 14 times more soil nitrogen (Table 4.6b). NF,IR plots had the highest soil nitrogen concentrations (58.2 µg/g) and NC,IC plots had the lowest levels with only 3.6 µg/g.

Individual species responses

Although most statistical analyses were done on plant functional groups, I did test for significant treatment responses of individual species. Individual species effects were difficult to assess because most species are not very abundant. However, in 2008 at Site 1, *Filago arizonica* percent cover was over twice as high in NC versus NF plots (H = 9.1, 3df, p = 0.0282; Table 4.7a), although the four treatments were not distinguishable using Tukey's HSD. For 2009 at Site 1, a Kruskal-Wallis test found that *Cryptantha angustifolia*, *Eriastrum diffusum*, *Loeseliastrum schottii*, and *Pectocarya heterocarpa* exhibited nitrogen treatment effects on percent cover. *E. diffusum* and *L. schottii* both had the highest percent cover in NC plots, while *C. angustifolia* and *P. heterocarpa* had higher percent cover in NF plots. However, *C. angustifolia* was the only species for which a Tukey's HSD corroborated the significant differences determined by the Kruskal Wallis test (H = 12.6, 3df, p = 0.0055; Table 4.7a). *C. angustifolia* was also the most abundant native annual species at Site 1 in 2009, with occupying an average percent cover of 20.3% in NF,IR plots. In 2010, *E. diffusum* was significantly different again (H = 12.4, 3df, 0.0061; Table 4.7a) and Tukey's HSD confirmed that percent cover was higher in NC plots. *Pectocarya linearis* had the highest percent cover in NF,IR plots, although treatments were not found to be different using Tukey's HSD (H = 9.6, 3df, p = 0.0224; Table 4.7a). The lack of agreement between the Kruskal-Wallis tests and Tukey's HSD are likely due to high variance and low abundance of the species.

Site 2 had fewer individual species responses to nitrogen fertilization and invasive removal. *Camissonia pallida* had significantly higher percent cover in NC plots in 2009 (H = 10.3, 3df, p = 0.0165; Table 4.7b) and *Pectocarya recurvata* followed the same pattern in 2010 (H = 10.1, 3df, p = 0.0177; Table 4.7b). *P. recurvata* is one of the most prevalent native annuals at Site 2 and Tukey's HSD confirmed that percent cover was almost seven times higher in NC,IC plots than NF,IC plots.

Fertile island experiment

Vegetative and soil measurements from NF,IC and NC,IC plots were compared to samples collected along shrub driplines. Invasive percent cover was lower in NC,IC plots compared to shrub understory plots, but was not significantly different from NF,IC plots (F-ratio = 5.8, 2df, p = 0.007; Figure 4.9), however native percent cover was not different. Both exotic invasive and native density were significantly higher in NC,IC plots than along shrub driplines (H = 11.3, 2df, p = 0.0036; H = 15.2, 2df, p = 0.0005; Figure 4.9), reaching almost three times the density of plants along shrub driplines. Species richness was not affected by any of the treatments, averaging between seven and eight species per plot (F-ratio = 0.2, 2df, p = 0.1499).

Invasive plant tissue nitrogen concentration was the same in all sampling locations ($p = 0.1552$). Therefore, although invasives experienced an increase in percent cover in shrub zones, they did not appear to assimilate extra nitrogen into leaf tissue. Native annual forbs, on the other hand, did assimilate more nitrogen into leaf tissue in NF,IC and shrub zones ($p = 0.0006$; Table 4.8). Invasive plant tissue C:N ratios were comparable in all three treatments and no differences were detected (F-ratio = 2.1, 2df, $p = 0.1552$; Table 4.8). However, native plant tissue C:N ratios were different, with the highest C:N in NC,IC plots (F-ratio = 11.5, 2df, $p = 0.0006$; Table 4.8); NF,IC and shrub dripline plots did not differ.

Aboveground tissue nitrogen did not differ between treatments and partitioning of aboveground nitrogen was not different between natives and invasives in any treatment. Tissue nitrogen ranged from 0.5 kg ha^{-1} in unfertilized plots to 2.0 kg ha^{-1} in fertilized plots (Table 4.9). Native and invasive productivity were lowest in NC,IC plots, while NF,IC and shrub zones were not different ($H = 20.5$, 2df, $p < 0.0001$; $H = 19.1$, 2df, $p < 0.0001$; Table 4.10).

Despite a general lack of vegetative differences, extractable soil nitrogen concentrations were higher in NF,IC plots than along shrub driplines. NH_4^+ concentrations were eight times higher in treated plots than shrub zones ($H = 17.6$, 2df, $p = 0.0001$; Table 4.9) and NO_3^- was five times higher ($H = 15.3$, 2df, $p = 0.0005$ Table 4.9).

Discussion

Nitrogen fertilization and invasive removal effects

Desert systems are limited by water and regulated by nitrogen. Without sufficient water availability, plants cannot utilize other resources, such as increased soil nitrogen. The positive plant responses to nitrogen in this study suggest that these sites in the Coachella Valley are not nitrogen saturated, despite the fact that they receive upwards of 9 kg ha^{-1} nitrogen per year (Tonnesen et al. 2007). Nitrogen pulses can heighten competitive interactions more than continuously available nitrogen, suggesting that temporal availability of nutrients is important (James and Richards 2006, James and Richards 2007). The duration of a nitrogen pulse is limited by factors such as plant uptake, microbial immobilization, volatilization and denitrification rates, and soil dry-down (James and Richards 2006, Rao and Allen 2010). In low nutrient, arid environments quick capture of nutrients is important. While all plants have some ability to respond to changes in nutrient availability, exotic invaders are often adept at obtaining and using water and nutrients more quickly than native species, thereby depriving them of valuable resources (Brooks 2000b, 2003, DeFalco et al. 2003, DeFalco et al. 2007). Based on this knowledge, I hypothesized that exotic invasive annuals would benefit from nitrogen fertilization and that native annual species would take advantage of increased soil nitrogen when invasive competition was reduced or eliminated, provided rainfall was adequate to allow it. This hypothesis was partially supported by my results, which also reinforced the highly variable nature of desert ecosystems.

In this study, the effects of nitrogen fertilizer and invasive removal varied by growing season and site. In 2008, invasive grass percent cover was significantly higher in fertilized plots, but neither invasive nor native annual forb cover was affected by the treatments. Invasive grass density also responded positively to nitrogen fertilizer. Native annual forbs, on the other hand, were significantly higher in unfertilized plots and invasive annual forbs were not affected. The contradictory responses of native forbs and invasive annual grasses to nitrogen fertilization suggest that the invasive grasses exert a stronger competitive effect on natives under fertilized conditions. However, this pattern did not always hold true for native annuals.

During the 2009 and 2010 growing seasons, when all exotic invasives were removed from IR plots, invasive percent cover was significantly higher in fertilized versus unfertilized IC plots. Despite the positive response from invasives and in contrast to 2008, native annuals also responded positively to nitrogen fertilization in the final two years of the study. The lag response of native annuals to increased soil nitrogen may be due to sequential years of nitrogen fertilization or a rebound effect from two years of invasive removal. In spite of the increased cover due to nitrogen, the pattern of native plant density found in 2008 persisted in 2009 but disappeared in 2010, when no significant density differences were detected between any treatment combinations. In both 2009 and 2010, invasive density was only affected by invasive removal treatments and not nitrogen. Therefore, although nitrogen has the ability to significantly increase native cover, it did not increase native density. Due to the relatively low cover and density of invasive plants at Site 1, it is unlikely that native density is hindered by invasive density in fertilized plots. Rather, native annual plants likely experienced enhanced growth and self-thinning effects under increased nitrogen, which explains an increase in percent cover but not density.

At Site 2, native and invasive percent cover and density numbers were more similar to each other than at Site 1 due to greater abundance of exotic invasive individuals. Native cover was highest in NF,IR plots in 2009, but was not significantly different from NF,IC or NC,IR plots, suggesting that the benefits of nitrogen fertilization were able to override competitive effects of exotic invasive species in NF,IC plots. By 2010, even native percent cover in NC,IC plots was not different from any other treatment combination. Contrastingly, native density was not affected by nitrogen or exotic invasive treatments in 2009, but was significantly lower in NF,IC in 2010. The fact that the only significant difference in native density was between NF,IR and NF,IC plots suggests that, although native density was higher than invasive density, the effect of exotic invasives in fertilized plots elicits a negative response from natives. This result is interesting because invasive density was not significantly higher in NF,IC plots when compared to NC,IC plots in 2010. This may be further evidence that nitrogen pulses can increase competition (James and Richards 2007).

Exotic invasive percent cover was only affected by invasive removal in 2009, but was significantly higher in NF plots as compared to NC plots in 2010. The response of exotic invasive cover to nitrogen in 2010 could be the result of nitrogen accumulation after three years of fertilization, or the above-average precipitation in the 2010 growing season may have allowed invasives to take full advantage of additional soil nitrogen. Invasive density was only affected by invasive removal treatments in both 2009 and 2010, suggesting that fertilization did not enhance germination and survival of new plants but allowed them to allocate resources to vegetative growth and, likely, higher seed production.

Tissue nitrogen concentration and tissue C:N ratios provided interesting insight into how nitrogen fertilizer and invasive removal affected tissue nutrients. Surprisingly, both invasive and native annual forb tissue nitrogen was higher in plots where invasive grass was not removed in 2008, suggesting that there may be some facilitative effect of exotic grass presence on native and invasive forb tissue nitrogen concentration. However, it is unlikely that this effect would be the same at sites where exotic grasses were more abundant, dominating competitors. This result is likely a reflection of the low density and percent cover of invasive grasses at the site rather than a demonstration of facilitative effects. Previous studies have shown that invasive annual grasses are effective competitors for soil nitrogen (Brooks 2003, Norton et al. 2007) and the results here may demonstrate the density-dependent nature of competition effects.

Although fertilization increased grass cover in 2008, C:N ratios were not different between control and fertilized plants at Site 1. Exotic invasives as a group were able to increase tissue nitrogen with fertilization in 2010, suggesting that the cumulative effects of repeated fertilization may have led to increased nitrogen acquisition by invasive plants. Native forbs were able to increase tissue nitrogen best under fertilized conditions, but the invasive removal effects differed between sites. At Site 1, where invasives were less abundant and removal had taken place for three years, nitrogen content was the lowest in NF,IC plots and was not significantly different from NF,IR or NC,IR plots. This finding mirrors the behavior of native percent cover at Site 1 in 2009 and implies that native annuals can compete with invasives for soil nitrogen, especially under fertilized conditions. At Site 2, native tissue from NF,IR plots was significantly lower than all other treatment combinations, as was tissue collected from NF,IC plots. This demonstrates that native annuals at Site 2 are able to effectively acquire nitrogen fertilizer whether or not exotic invasives are removed, although they are slightly affected by invasive competition in IC plots. These results are important because invasive species are well known for having the ability to compete with natives for soil nutrients (Brooks 2003, DeFalco 2003, DeFalco et al. 2007), however these data demonstrate that native desert annuals are also able to successfully acquire additional soil nitrogen in the field. Furthermore, it appears that when invasive plants occur at relatively low densities native annuals are able to co-exist with invasives or even overcome competitive effects by utilizing increased soil nitrogen.

Comparisons between native and invasive tissue C:N elicited enlightening results, as well. First, significant differences were only detected in 2008 at Site 1 (Table 4.11). In all other years and treatments, native and invasive tissue C:N ratios were indistinguishable (Table 4.11). In 2008, only invasive grasses were removed from IR plots and C:N was tested for three functional groups: invasive grass, invasive forb, and native forb. Invasive forbs appeared to be the most effective at taking up soil nitrogen.

Invasive forbs had significantly higher tissue nitrogen concentration than invasive grasses and native forbs under every treatment combination except NF,IC, where no significant differences were found. In the face of a changing exotic invasive community, these results suggest that invasive forbs may be more competitive in terms of nitrogen uptake and storage within plant tissue.

When comparing native and invasive forbs, the differences in nutrient allocation may be related to the structural framework of the dominant species. *E. cicutarium* is the dominant invasive forb at Site 1 and has a prostrate basal rosette, which is mostly senesced by the time of flowering and fruiting. Its litter also disarticulates fairly quickly. However, the dominant native annuals at Site 1 in 2008 were *Cryptantha angustifolia*, *Pectocarya recurvata*, and *P. heterocarpa*. These plants have much tougher structural integrity with small leaves and fibrous stems; they also leave behind semi-persistent standing litter at the end of the growing season. These structural differences between functional groups may account for the allocation of native annuals to carbon and the significantly higher tissue nitrogen concentration of invasive forbs. Nevertheless, invasive forbs have the ability to take up large amounts of soil nitrogen and render it unavailable to natives.

Native annual plant productivity was always highest in NF plots. At Site 1, native annuals were significantly more productive in NF,IR plots, however invasive removal was not important for native productivity at Site 2. This highlights the complexity of plant interactions and the importance of site-specificity because Site 2 had much higher invasive density than Site 1, but this did not affect the productivity of native annuals there. Exotic invasive annuals were always most productive in NF,IC plots at both sites, demonstrating that they were able to take advantage of nitrogen fertilization but did not exert a strong competitive effect on natives at Site 2.

Competitive interactions are contingent on a combination of biotic and abiotic factors and low invasive plant densities at these sites often negated any competitive effect they may have had. In this study, we used vegetative responses to extrapolate potential competitive ability of native and invasive plants. Invasive percent cover responded to nitrogen four out of five times and although native species cover only increased three out of five times, native cover and density almost always exceeded that of invasives. Furthermore, the positive responses of invasives to nitrogen fertilization did not seem to increase the invasive species seed bank, even after three years of fertilization at Site 1. In fact, Site 2 saw a nearly 50% decrease in invasive plant density from 2009 to 2010. This supports the idea that if repeated nitrogen fertilization does alter soil seed bank composition or density, it may take several years before the change is apparent (Schneider chapter 1).

Despite the relatively low competitive impact of invasive species at this site, it is important to note that the ability of *E. cicutarium* to take up added nitrogen may lead to increased competitive ability under higher densities than were found at these two sites. In a greenhouse study, *E. cicutarium* was found to consistently garner advantages of increased water and nitrogen to a greater extent than native annual species (Schneider 3).

This points to the potential dominance of *E. cicutarium*, especially under high water and nitrogen, in sites where it is an abundant invader, as well as the potential importance of resource variability for the persistence of native annual species.

Although analysis of individual species was limited, it provided some insights into how nitrogen fertilization and invasive removal affect native annuals at the species level. One of the most important patterns that can be discerned from native species responses to the treatments is that some species had different responses to nitrogen fertilization. Some species had the highest percent cover in fertilized plots, while others had higher percent cover in control plots. Thus, although native annual forbs as a group tended to respond positively to nitrogen additions, individual species may respond adversely. This suggests that it is possible that prolonged exposure to increased soil nitrogen could shift native annual species composition, which has been demonstrated by other studies (Bobbink et al. 1998, Clark and Tilman 2008).

The effects of drought on invasive grass populations and species shifts

Herbicide application was originally intended to control exotic invasive grasses, but during the course of the experiment there was a shift in the invasive community from grasses to *Erodium cicutarium*. Annual plants in California have high annual variation in composition and abundance (Talbot et al. 1939). Desert annual plant communities can vary greatly in species composition from one year to the next, which may be linked to environmental cues for germination such as temperature and amount and timing of precipitation, as well as biotic factors such as seed predation and seedling density (Went 1949, Inouye et al. 1980, Pake and Venable 1996, Brooks 2003). Precipitation was average in 2008 and 2009, with 10.6 and 10.8 cm of rainfall, respectively. In 2010, precipitation was slightly above average and more than 50% higher than the previous two seasons (18.3 cm). The years of this study were preceded by one of the wettest years on record (2004-2005: 32.4 cm) and two years of drought, which led to almost no plant production (2005-2006: 5.6 cm; 2006-2007: 2 cm). Following the two years of drought, the invasive plant community shifted from being previously dominated by invasive grass to an increased abundance of invasive forbs, especially *Erodium cicutarium*. Invasive grass population 'crashes' have been observed following multi-year droughts because of reduction in seed banks (Brooks 2000a, Salo 2004, Minnich 2008) while the invasive forbs *E. cicutarium* and *B. tournefortii* have more persistent seed banks that survive drought years (Mayor et al. 1999, Marushia 2009).

Due to this shift in the abundance and composition of invasives at Site 1, the experimental treatments were altered to effectively control the new exotic invasive community. Originally, the invasive removal treatment consisted of the application of Fusilade II®, a grass-specific herbicide. In 2009 and 2010, a combination of herbicide and hand weeding was used to remove all aboveground invasives from study plots.

Non-target effects of Fusilade II®

Although the herbicide treatment was intended to target exotic invasive annual grass species, previous studies have found that the family of herbicides Aryloxyphenoxy-propionate, which includes Fusilade II® (Fluazifop-P-butyl), can also be effective on *Erodium* species (Christopher and Holtum 1998, 2000, Steers 2008, Steers and Allen 2010). *E. cicutarium* is present at both sites and the native annual forb *Erodium texanum* has been found at Site 1, although it was not observed at the time of herbicide application. The susceptibility of *Erodium* species to this 'grass-specific herbicide' is due to a lack of the multi-subunit form of acetyl coenzyme A carboxylase (MS ACCase), which is typically present in most plants (Christopher and Holtum 2000). In this study, *E. cicutarium* was not completely controlled by Fusilade II® application, but it was negatively affected (H. Schneider personal observation). Most of the affected plants were not killed, although some small individuals did appear to die from exposure to herbicide. Damaged *E. cicutarium* foliage appeared red and often had curled leaves. Between 50 and 80% of *E. cicutarium* individuals appeared to be damaged or killed by Fusilade II® over the course of the study. Fusilade II® was very effective at removing invasive grass individuals, with virtually zero survival rates post-application. It is unclear whether Fusilade II® could effectively control *E. cicutarium* in the desert based on the results of this study because damaged individuals were removed from plots one week after herbicide application, however other studies have suggested that Fusilade II® may offer land practitioners an addition tool that could control both invasive grasses as well as *E. cicutarium* (Steers and Allen 2010).

Nitrogen fertilization and the fertile island effect

The so-called ‘fertile island effect’ is an important phenomenon in desert scrub communities. The areas beneath and surrounding shrubs offer native annual plants a reprieve from the low nutrients, extreme sunlight, temperatures, and aridity of the interspaces between shrubs. In this experiment, I used vegetation and soil measurements to determine whether or not nitrogen fertilization could simulate the benefits of the fertile island effect in the interspace. I found that NF,IC plots were similar in vegetation to shrub zones. Furthermore, NC,IC plots tended to be different from NF,IC plots and shrub zones, highlighting that the differences are likely due to increased soil nitrogen. Percent cover was not significantly different between the two sampling locations, although NF,IC plots had significantly higher native and invasive plant density than shrub zones. This indicates that plants in NF,IC plots were smaller and more numerous, while plants in shrub zones increased in size rather than number. Tissue C:N and plot productivity also did not differ between treatment plots and shrub zones, although extractable soil nitrogen was higher in fertilized plots. These results suggest that nitrogen fertilization in the interspace can evoke a plant response that mimics the fertile island effect, despite the advantages of shade and increased soil moisture found near shrubs. Furthermore, although extractable soil nitrogen in NF,IC plots reached levels up to five times that of shrub zones, this additional nitrogen did not appear to confer any additional benefit to interspace vegetation. In light of this fact, it is likely that there is a threshold amount of soil nitrogen that can be effectively utilized and that once the system is saturated, no further benefits can be incurred.

Implications for conservation and restoration

Desert annual communities are highly variable and specially adapted to deal with the harsh abiotic environment in which they exist. Erratic precipitation events combined with low soil nutrient levels have created a community of native annuals that is fairly conservative with respect to germination and growth. Factors such as timing of precipitation and temperature at the time of precipitation can also impact the germination of native annual seeds. The variability in results from this study, even in years with comparable precipitation, demonstrates the complex interactions that control annual plant communities. While annual species can account for up to 40% of the plant population in the desert, their presence aboveground fluctuates based on specialized germination cues that will release them from the soil seed bank (Kemp 1989). During periods of low rainfall or drought, some species may not appear aboveground for years as they lie in wait for more favorable conditions. For this reason, it can be difficult to study native annual communities in deserts. While this study is not a comprehensive assessment of the effects of anthropogenic nitrogen deposition and exotic invasive species on native annuals, it does offer some important insights that may be applicable to land managers, as well as a jumping off point for future research.

Studies have shown that exotic invasive species and anthropogenic nitrogen deposition can have detrimental effects on native plants (Allen et al. 1997, Brooks 2000b, Rao 2008, Steers 2008, Allen et al. 2009). Understanding how to manage or mitigate these impacts is important for conserving and restoring disrupted communities. One major concern in Southern California is the increased fire risk associated with exotic invasion (Brooks 1999a, Rao 2008, Steers 2008). Exotic annual invasions in the desert can increase fire frequency and intensity (Brown and Minnich 1986, Brooks et al. 2004, Brooks and Minnich 2006), which threatens native desert plant communities. Fire is historically rare in creosote bush scrub communities, rendering them poorly adapted to large or frequent fires (Brown and Minnich 1986, Brooks 2002, Steers 2008). In low productivity communities, exotic invaders have the capacity to increase community productivity and create a fine fuel layer that connects otherwise disconnected shrubs (Brooks 1999a, Schutzenhofer and Valone 2006). However, it is unlikely that exotic invasion will lead to increased fire at these sites due to relatively low plant productivity, even under high nitrogen conditions. Fire thresholds have been suggested for assessing fire risk in wildlands. One study examining the effects of nitrogen and watering treatments on desert annual productivity suggested using a fire threshold of one ton per hectare and determined that creosote bush scrub communities can rarely surpass the threshold, even under extreme water and nitrogen inputs (Rao et al. 2010). In this study, maximum biomass was achieved in fertilized plots but never exceeded 500 kg ha^{-1}, which is half of the plant biomass required to carry a fire.

The exotic invasive removal treatments used in this study also offer lessons for invasive species management. The combination of herbicide application and hand weeding was extremely effective in removing invasive species from treatment plots and also appeared to have a cumulative effect over consecutive years. Invasive density was fairly low throughout the study and, after three years of exotic invasive removal, invasive grasses and forbs were exceptionally scarce in IR plots. Despite the fact that hand-weeding wildland areas is not a practical approach to invasive species eradication, the results of this study suggest that multi-year control efforts may have cumulative or lasting effects on their abundance. This study also demonstrates that complete removal of invasive species is not necessary for native annuals to take advantage of increased soil resources. In fact, some studies have found that low density populations of exotic invaders can offer some facilitative effect to natives (Rodriguez 2006, Schutzenhofer and Valone 2006). Further research about invasive density thresholds for competition could offer land managers valuable information for conservation and restoration. Since natives at these sites were less affected by low densities of invasives, determining an ‘acceptable’ level of invasion could allow land managers to design programs aimed at invasive reduction, rather than eradication, which is often more realistic on the large scale of natural systems.

Prior to the collection of field data, a marked shift in the species composition and density of the exotic invasive community occurred, likely due to two consecutive years of drought. This pattern has been observed before (Salo 2004, Minnich 2008) and demonstrates that the natural stochasticity of the desert may offer a temporal safe haven for native species. One caveat to this, however, is the fact that invasive forbs like *E. cicutarium* have the ability to seed bank and are not likely to be as susceptible to drought as other exotic invaders. Nevertheless, other characteristics of exotic invaders such as early germination and rapid phenology do offer managers an opportunity to control invasives with minimal impact to native populations. Control efforts should take into account the windows of opportunity offered by functional differences between invasives and natives and also be conscious of the variability between growing seasons. Restoration and conservation plans are likely to be the most successful when tailored to individual sites rather than subscribing to a more general protocol.

Finally, the generally positive response of native annuals to increased soil nitrogen is an important finding. This is not to say that anthropogenic nitrogen deposition does not pose a threat to native plant communities, rather this study demonstrates that increased soil nitrogen does not always create a positive feed back cycle for invasives only. Indeed, in areas where invasives are less prevalent or have been successfully controlled, native annuals are able to benefit from nitrogen additions (Allen et al. 2009). However, many areas of the desert are invaded with dense stands of invasives, which prevent or negate any positive influence of added nitrogen on native species. Furthermore, increased soil nutrients can assist in range expansion of invasive species by alleviating the stress of impoverished desert soils. Hence, it is imperative for regulators to recognize the urgent need for nitrogen emissions legislation in order to protect the valuable ecosystem services that native wildlands provide.

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Figure 4.1. Plots at both sites were set up using a randomized block design. Each site was made up of 12-5x5 m blocks containing 4-1x1 m plots each. All treatment combinations were represented in each block (NF = nitrogen fertilized, NC = nitrogen control; IR = invasive removal, IC = invasive control). The arrow points to an enlarged version of one plot within the block and indicates which types of samples were collected and where those samples were collected each year.

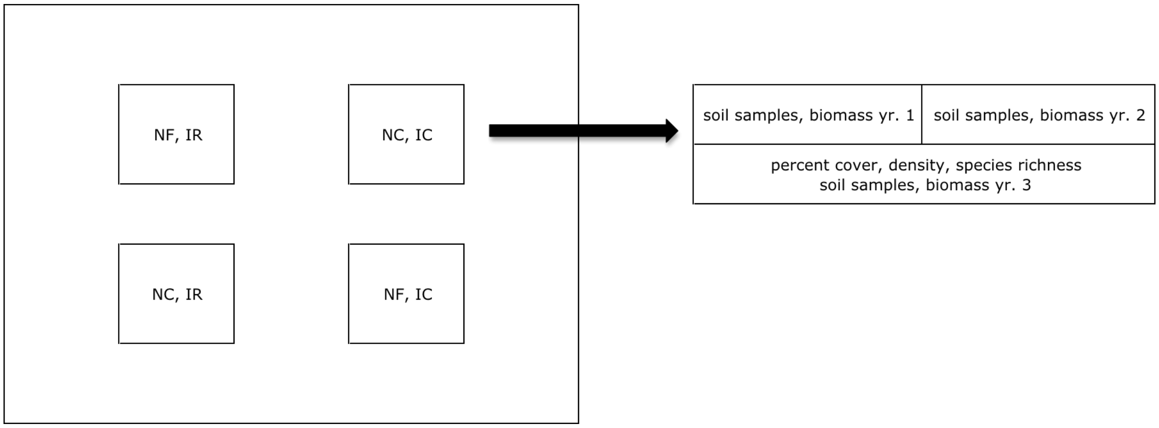
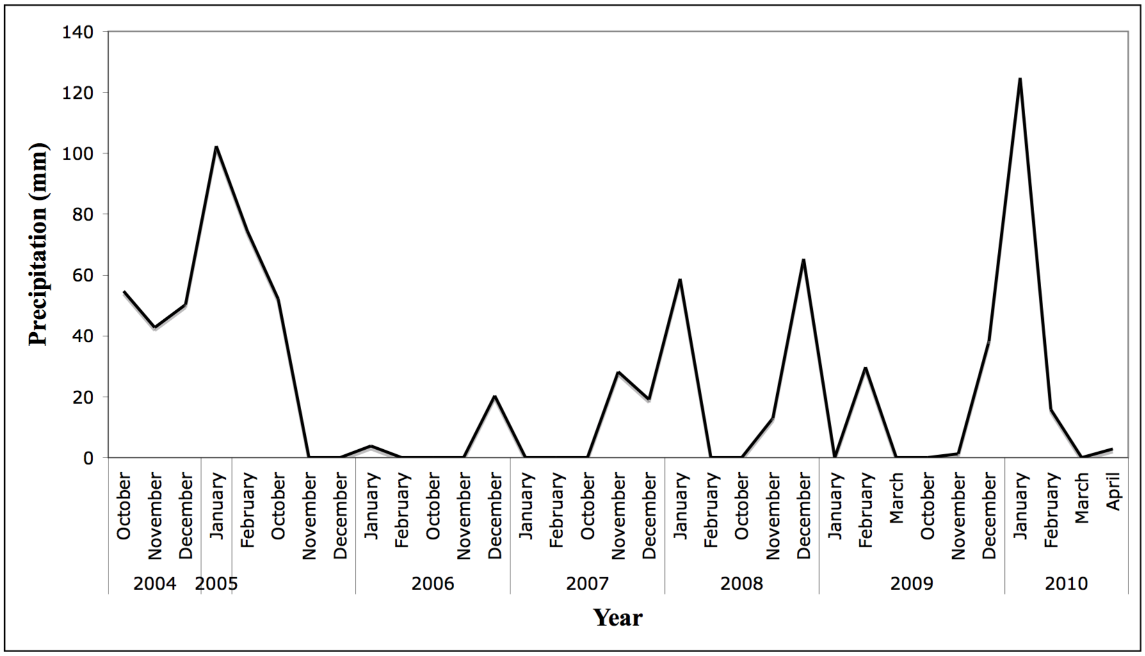


Figure 4.2. Precipitation data was collected from the National Oceanic and Atmospheric Administration (NOAA) for the Palm Springs weather station. All precipitation fell as rain and is reported in millimeters. Total precipitation for each growing season was calculated as the summation of all measurable precipitation that fell between October and April.



Growing season	Total precipitation
2004 - 2005	324
2005 - 2006	56
2006 - 2007	20
2007 - 2008	106
2008 - 2009	108
2009 - 2010	183

Table 4.1. Species occurrences at sites 1 and 2 according to functional group, family, and species for each of the three growing seasons of the study. Values represent average percent cover for NC,IC plots; asterisks (*) denote species found only in treatments other than NC,IC. NC = nitrogen control, IC = invasive control.

			2008	**2009**		**2010**	
Functional Group	**Family**	**Species**	**Site 1**	**Site 1**	**Site 2**	**Site 1**	**Site 2**
Invasive grass	Poaceae	*Schismus* spp.	2.15	3.67	5.33	1.94	0.99
Invasive forb	Brassicaceae	*Brassica tournefortii*	0.8	1.62	0.04	1	0.13
	Geraniaceae	*Erodium cicutarium*	1.03	2.16	12.33	2.69	10.25
Native forb	Asteraceae	*Chaenactis fremontii*	0	0.01	2.05	0.02	3.23
		Filago arizonica	1.33	0	0	1.54	0.06
		Filago depressa	0	1.04	0.13	0.22	0
		Malacothrix glabrata	0*	0.37	0*	0.08	0.53
		Stephanomeria exigua	0	0.6	0	0.69	0
		Rafinesquia neomexicana	0.17	0	0.75	0*	0
	Boraginaceae	*Cryptantha angustifolia*	7.92	7.77	0.88	3.67	0.08
		Cryptantha micrantha	0.03	0.05	0	0.02	0
		Pectocarya heterocarpa	5.88	2.68	0.73	8.88	2.88
		Pectocarya linearis	0.08	0.02	2.71	0*	5.29
		Pectocarya penisularis	0	0	0	0*	0
		Pectocarya platycarpa	0.17	0.08	0.19	0.11	0.03
		Pectocarya recurvata	0.12	0.1	7.65	1.13	8.42
	Brassicaceae	*Lepidium lasiocarpum*	0	0	0*	0.17	0*
	Caryophyllaceae	*Achyronychia cooperi*	0.02	0.02	0.08	0.18	0
		Loeflingia squarrosa	0.25	0.35	0	0.32	0
	Crassulaceae	*Crassula connata*	0.17	0.2	0*	1.08	0.01
	Fabaceae	*Astragalus didymocarpus*	0	0	0	0.04	0
	Geraniaceae	*Erodium texanum*	0	0*	0	0*	0
	Malvaceae	*Eremalche exilis*	0*	0*	0	0.03	0
	Onagraceae	*Camissonia claviformis*	0.18	0*	0.02	0*	0*
		Camissonia pallida	2.37	0.76	0.06	0.81	0.17
	Plantaginaceae	*Plantago ovata*	0.1	0.21	0	0.02	0
		Plantago spp.	0*	0	0	0	0
	Polemoniaceae	*Eriastrum diffusum*	2.08	4.75	0	3.17	0
		Loeseliastrum schottii	0.29	0.2	0.65	0.3	0.37
	Polygonaceae	*Chorizanthe brevicornu*	0.09	0.26	1.28	0.49	0.33
	Portulacaceae	*Calyptridium monandrum*	0.86	0.19	0*	0.98	0*

Figure 4.3. Percent cover of native and exotic vegetation at Site 1 in 2008. Percent cover was compared within functional groups by treatment. Significant differences were determined using a Tukey's HSD test ($p = 0.05$); values separated by different letters are significantly different. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = invasive removal.

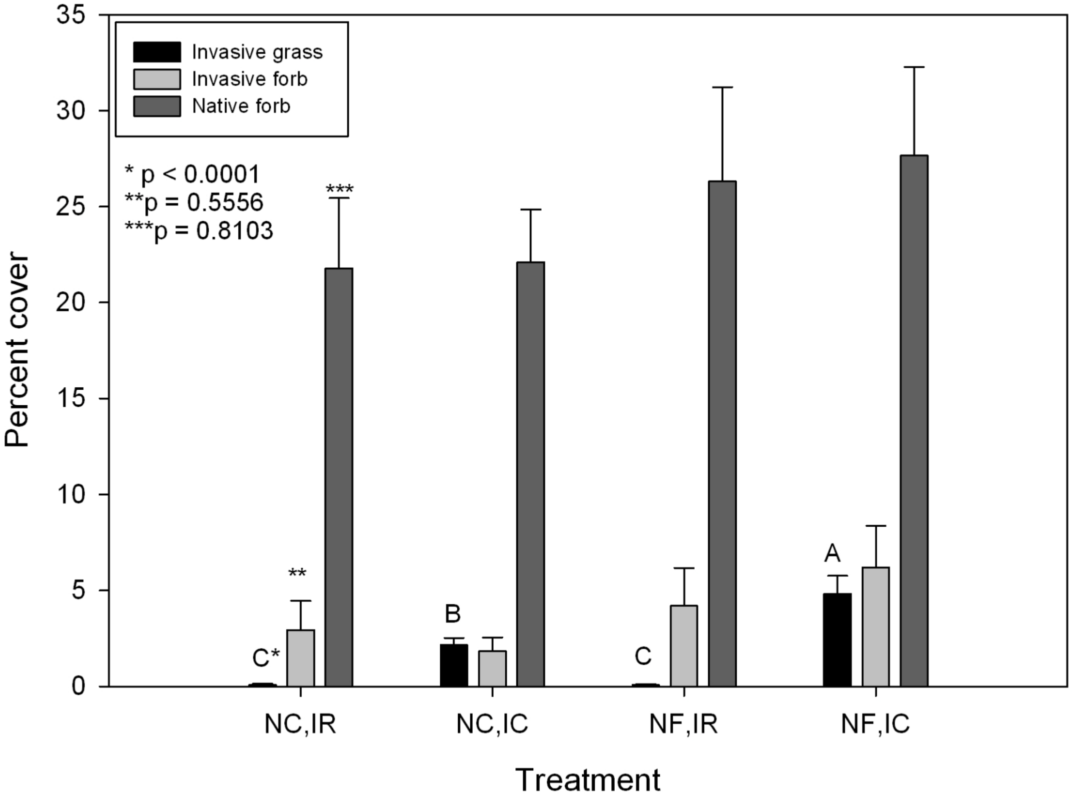


Figure 4.4. Plant density per m^2 by functional group for each treatment at Site 1 in 2008. Significant differences were determined using Tukey's HSD (p = 0.05); values separated by different letters are significantly different. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = invasive removal.

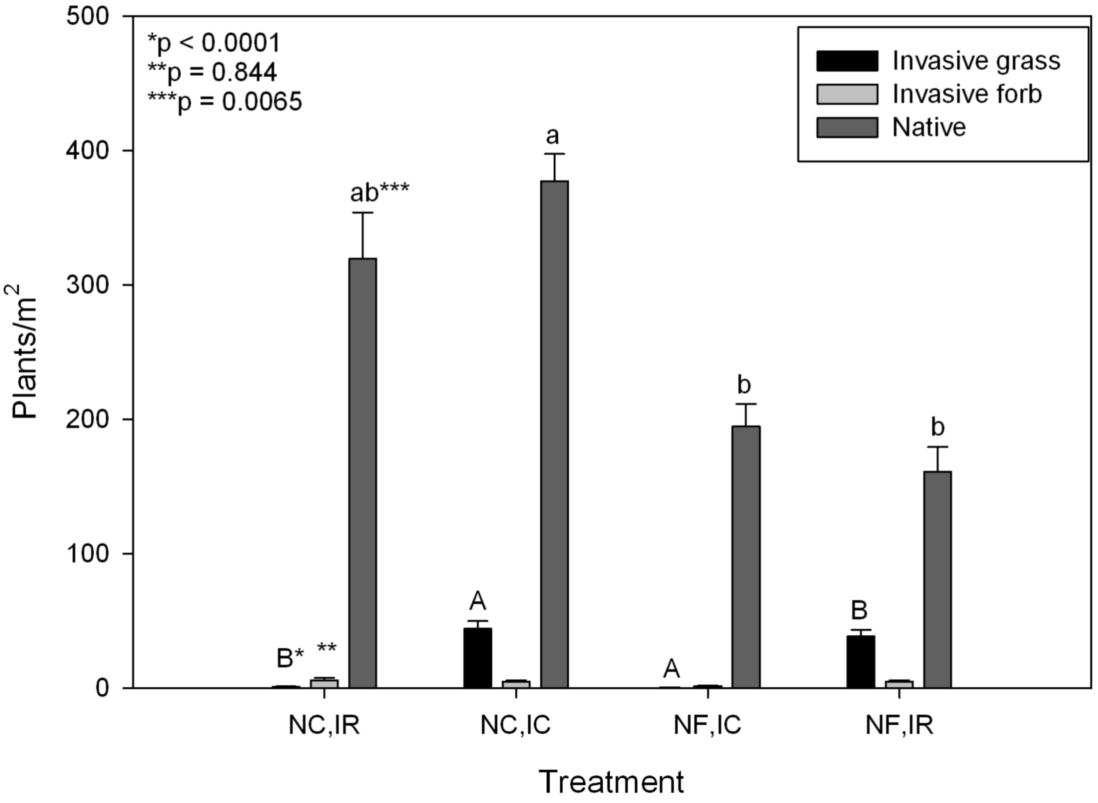


Table 4.2. Total species richness at each site within treatments by year. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = invasive removal. Significant differences were determined using a two-way ANOVA and Tukey's HSD and are denoted by an asterisk (*).

Site	Year	Treatment	Richness	Significance	Source	F-ratio	p-value
Site 1	2008	NC,IR	9.7	A	Whole model	0.758	0.523
		NC,IC	10	A	Nitrogen	1.85	0.1812
		NF,IR	8.9	A	Exotic	0.43	0.5163
		NF,IC	9.4	A	Nitrogen*Exotic	0.0017	0.9674
	2009	NC,IR	9.4	B	Whole model	3.57	0.0215*
		NC,IC	11.1	A	Nitrogen	0.0052	0.9428
		NF,IR	8.5	B	Exotic	2.76	0.1038
		NF,IC	10.1	AB	Nitrogen*Exotic	7.93	0.0072*
	2010	NC,IR	10	B	Whole model	3.08	0.037*
		NC,IC	12.4	A	Nitrogen	0.2197	0.6416
		NF,IR	10.3	B	Exotic	8.18	0.0064*
		NF,IC	11.4	AB	Nitrogen*Exotic	0.842	0.3637
Site 2	2009	NC,IR	8.5	A	Whole model	2.13	0.1095
		NC,IC	8.3	A	Nitrogen	3.97	0.0525
		NF,IR	7	B	Exotic	0.821	0.3699
		NF,IC	8	AB	Nitrogen*Exotic	1.61	0.2113
	2010	NC,IR	7.1	B	Whole model	5.13	0.004*
		NC,IC	8.3	A	Nitrogen	8.12	0.0066*
		NF,IR	6	B	Exotic	7.21	0.0102*
		NF,IC	7	B	Nitrogen*Exotic	0.05	0.8183

Table 4.3. Shannon-Wiener Diversity and Pielou's Evenness indices were calculated at each site by treatment. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = invasive removal.

Site	Year	Treatment	Shannon-Wiener Diversity (H')	Pielou's Evenness (J')
Site 1	2008	NC,IR	1.99	0.88
Site 1	2008	NC,IC	2.05	0.89
Site 1	2008	NF,IR	1.82	0.83
Site 1	2008	NF,IC	2.18	0.97
Site 1	2009	NC,IR	1.9	0.85
Site 1	2009	NC,IC	2.1	0.87
Site 1	2009	NF,IR	1.72	0.80
Site 1	2009	NF,IC	2.07	0.90
Site 2	2009	NC,IR	1.96	0.91
Site 2	2009	NC,IC	1.61	0.76
Site 2	2009	NF,IR	1.51	0.78
Site 2	2009	NF,IC	1.71	0.82
Site 1	2010	NC,IR	2.18	0.95
Site 1	2010	NC,IC	2.25	0.89
Site 1	2010	NF,IR	2.18	0.94
Site 1	2010	NF,IC	2.18	0.89
Site 2	2010	NC,IR	1.86	0.95
Site 2	2010	NC,IC	1.69	0.80
Site 2	2010	NF,IR	1.46	0.82
Site 2	2010	NF,IC	1.63	0.84

Table 4.4 a & b. Total aboveground nitrogen and productivity of a) native and b) invasive plants. The data were analyzed using a Kruskal-Wallis and Tukey's HSD (α = 0.05) to determine significant differences (denoted by *). No biomass was collected in 2009. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = invasive removal.

a)

Site	Year	Treatment	Aboveground N (kg ha^{-1})	Significance	p-value	Biomass (kg ha^{-1})	Significance	p-value
Site 1	2008	NC,IR	2	A	0.0588	105	A	0.2347
		NC,IC	4.1	A		159.8	A	
		NF,IR	3.4	A		146.2	A	
		NF,IC	3.6	A		134	A	
	2010	NC,IR	2.3	BC	<0.0001	68.6	B	< 0.0001*
		NC,IC	1.7	C		55.4	B	
		NF,IR	6.5	A		178	A	
		NF,IC	4.4	AB		102.6	B	
Site 2	2010	NC,IR	0.81	C	<0.0001*	110.8	B	< 0.0001*
		NC,IC	0.7	C		101.8	B	
		NF,IR	3.8	A		258.8	A	
		NF,IC	2	B		196.4	A	

b)

Site	Year	Treatment	Aboveground N (kg ha-1)	Significance	p-value	Biomass (kg ha-1)	Significance	p-value
Site 1	2008	NC,IR	1.7	A	0.171	6.4	A	0.5079
		NC,IC	0.7	A		7.6	A	
		NF,IR	0.55	A		18.2	A	
		NF,IC	1.1	A		22.4	A	
	2010	NC,IC	0.63	A	<0.0001*	21	B	< 0.0001*
		NF,IC	3	B		58.8	A	
Site 2	2010	NC,IC	0.39	A	<0.0001*	46.4	A	< 0.0001*
		NF,IC	2	B		187.8	B	

Table 4.5. Tissue nitrogen concentration and tissue C:N ratios for each site by year and functional group. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = Invasive removal. Significant differences were determined using factorial ANOVA or Kruskal-Wallis test for nonparametric data (p = 0.05; denoted by *).

Site	Year	Functional Group	Treatment	Tissue %N	Significance	Source	p-value	C:N (SE)	Significance	Source	p-value
Site 1	2008	Invasive grass	NC,IC	1.1 (0.07)	A	Nitrogen, Invasive	0.5395	14.3 (0.9)	A	Nitrogen,Invasive	0.614
			NF,IC	1.2 (0.1)	A			13.5 (1.2)	A		
		Invasive forb	NC,IR	0.91 (0.09)	A	Whole model	0.0154*	15 (1.2)	A	Whole model	0.0262*
			NC,IC	1.4 (0.1)	AB	Nitrogen	0.4664	9.5 (1.3)	B	Nitrogen	0.9486
			NF,IR	1.1 (0.07)	B	Invasive	0.0301*	12.03 (0.7)	AB	ExoticInvasive	0.0477*
			NF,IC	1.1 (0.1)	AB	Nitrogen * Inv.	0.0176*	12.6 (1.3)	AB	Nitrogen*Inv.	0.0171*
		Native forb	NC,IR	0.63 (0.05)	A	Whole model	0.0016*	20.2 (1.2)	A	Whole model	0.0019*
			NC,IC	0.91 (0.07)	B	Nitrogen	0.0468*	15.3 (1)	B	Nitrogen	0.0629
			NF,IR	0.82 (0.06)	AB	Invasive	0.0011*	16.9 (1.2)	B	Invasive	0.0012*
			NF,IC	0.96 (0.06)	B	Nitrogen * Inv.	0.2735	14.6 (0.9)	B	Nitrogen*Inv.	0.2222
	2010	Invasive	NC,IC	1.5 (0.3)	A	Nitrogen, Invasive	0.0001*	28.2 (1.6)	A		0.0012*
			NF,IC	2.6 (0.2)	B			18.4 (0.9)	B		
		Native forb	NC,IR	1.7 (0.3)	AB	Whole model	0.0165*	24.4 (1.6)	AB		0.0427*
			NC,IC	1.5 (0.09)	A	Nitrogen	0.0056*	27.67 (1.8)	A		
			NF,IR	1.8 (0.07)	AB	Invasive	0.6855	23 (1.04)	AB		
			NF,IC	2.2 (0.2)	B	Nitrogen * Inv.	0.0924	20.7 (1.7)	B		
Site 2	2010	Invasive	NC,IC	1.7 (0.2)	A	Nitrogen, Invasive	0.1099	27 (2.6)	A		0.0929
			NF,IC	2.1 (0.2)	A			21.2 (1.5)	A		
		Native forb	NC,IR	1.5 (0.1)	A	Whole model	< 0.0001*	29.7 (2.1)	A		< 0.0001*
			NC,IC	1.4 (0.06)	A	Nitrogen	< 0.0001*	30.2 (1.1)	A		
			NF,IR	2.9 (0.2)	B	Invasive	0.005*	16.3 (0.7)	C		
			NF,IC	2 (0.1)	C	Nitrogen * Inv.	0.0215*	21.9 (1.4)	B		

Figure 4.5 a & b. Percent cover was measured by functional group in a) 2009 and b) 2010 for each treatment at Site 1. Significant differences were determined using Tukey's HSD (p = 0.05); values separated by different letters are significantly different. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = invasive removal.

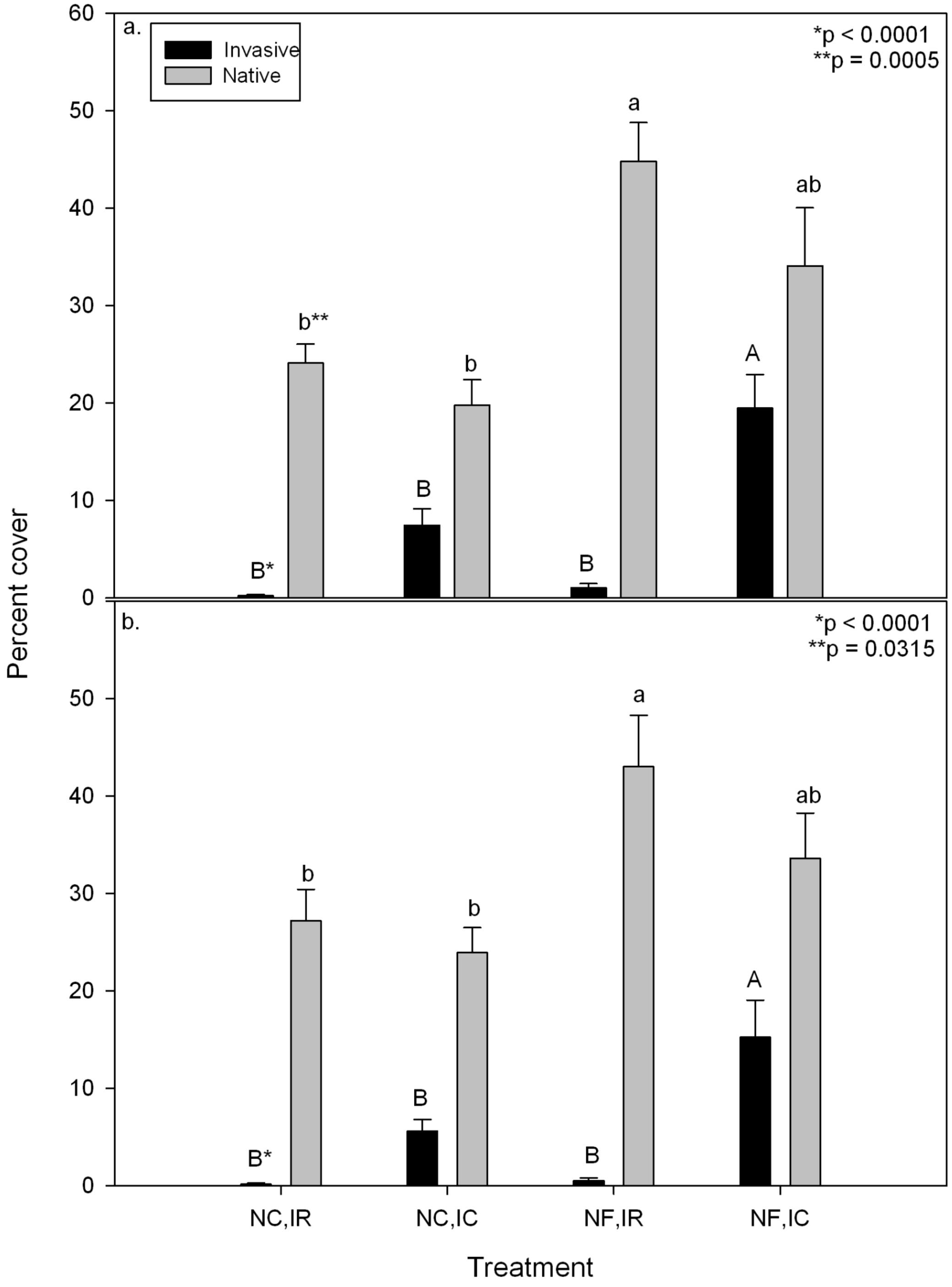


Figure 4.6 a & b. Plant density per m^2 by functional group for each treatment at Site 1 in a) 2009 and b) 2010. Significant differences were determined using Tukey's HSD ($p = 0.05$); values separated by different letters are significantly different. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = invasive removal.

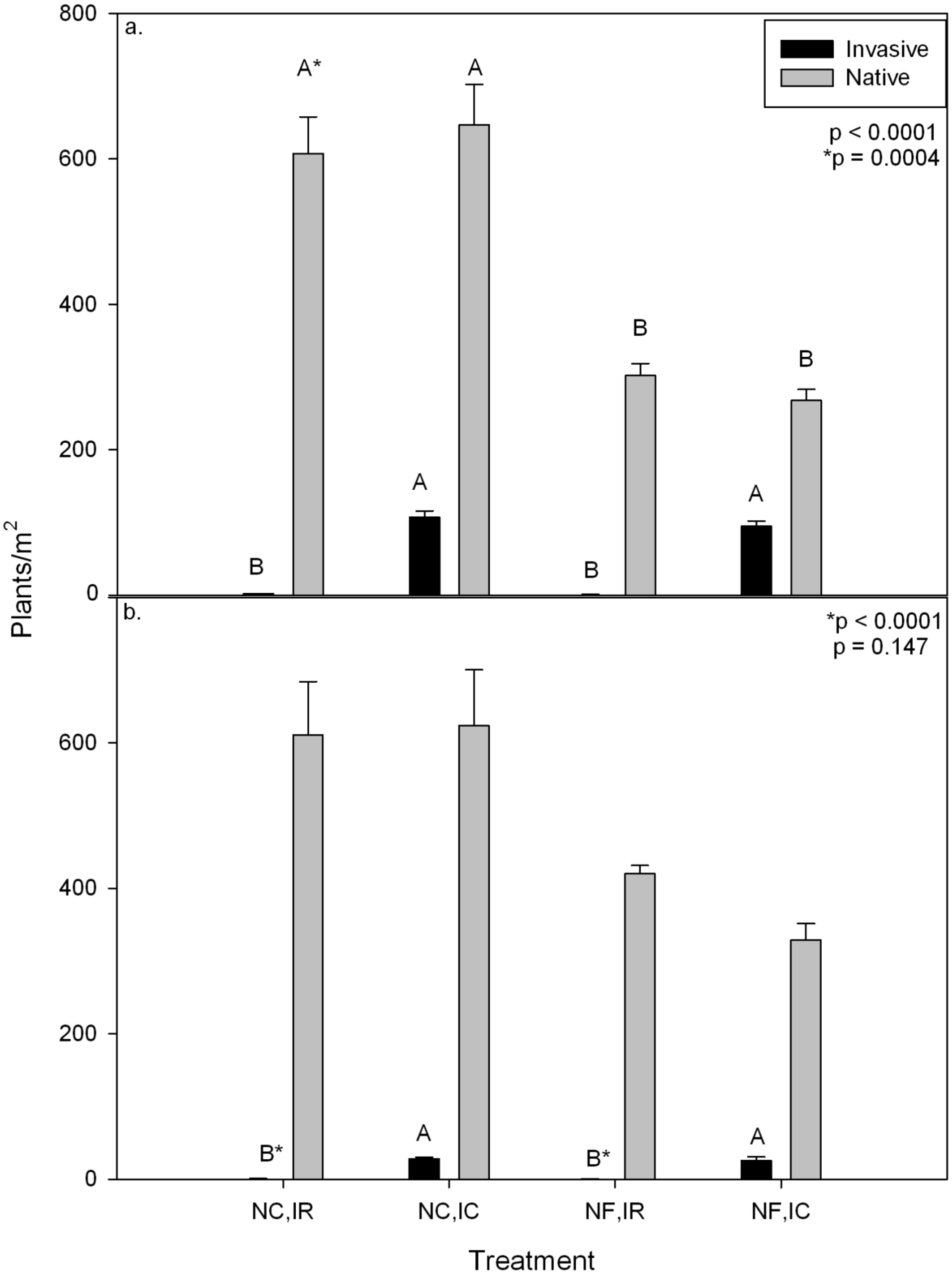


Figure 4.7 a & b. Percent cover was measured by functional group in a) 2009 and b) 2010 for each treatment at Site 2. Significant differences were determined using Tukey's HSD (p = 0.05); values separated by different letters are significantly different. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = invasive removal.

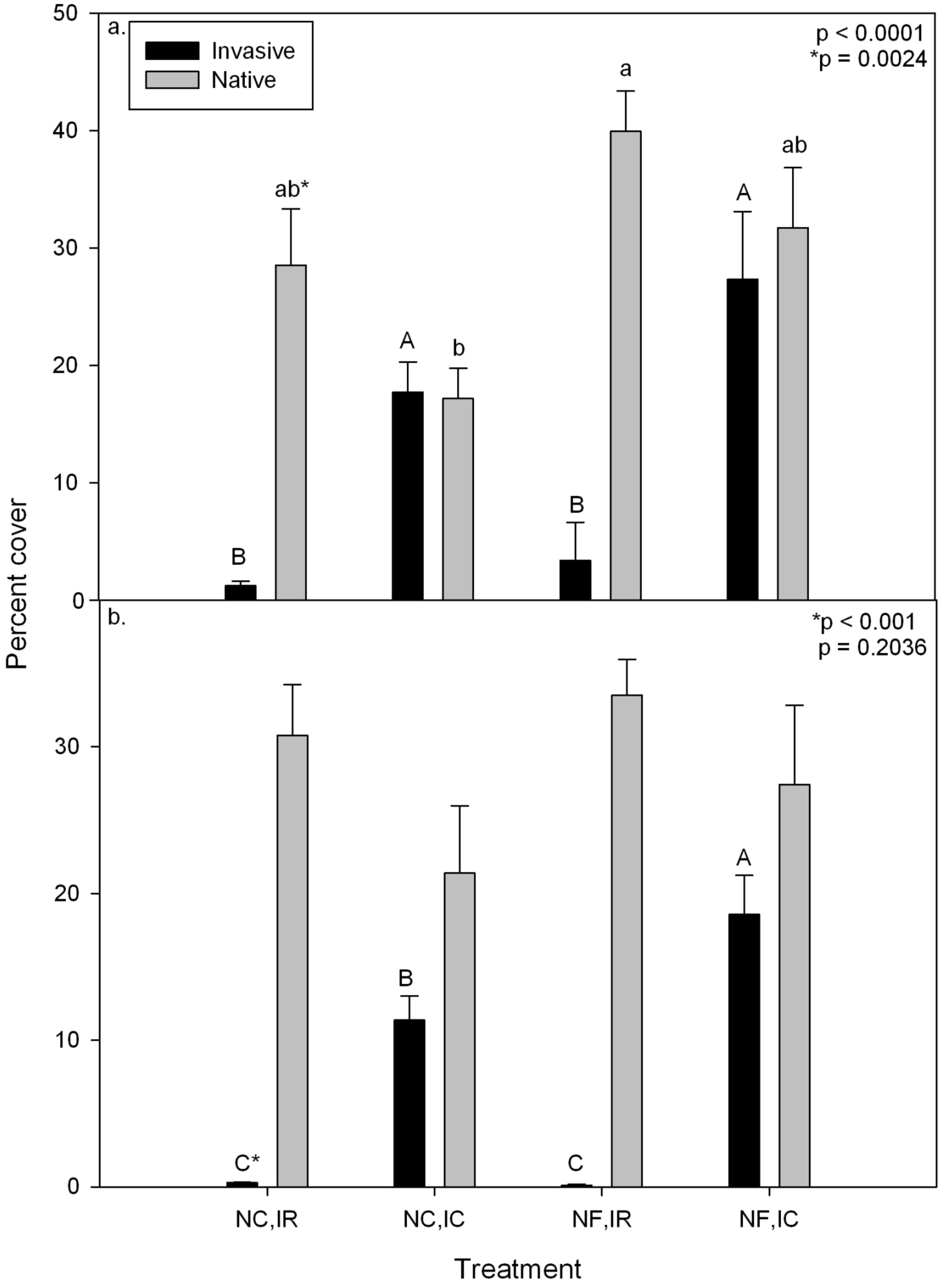


Figure 4.8 a & b. Plant density per m^2 by functional group for each treatment at Site 2 in a) 2009 and b) 2010. Significant differences were determined using Tukey's HSD (p = 0.05); values separated by different letters are significantly different. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = invasive removal.

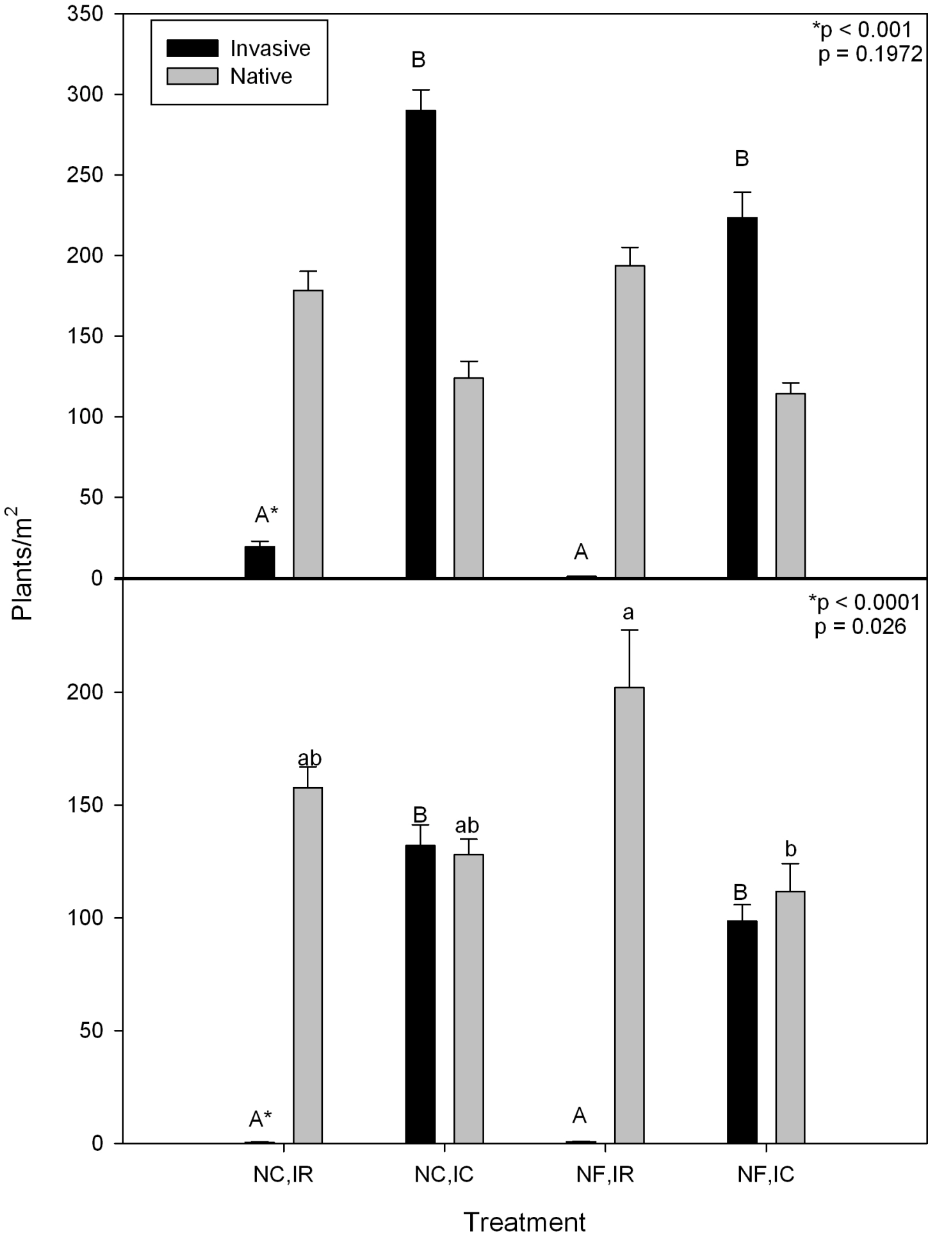


Figure 4.9. NF,IC, NC,IC plots, and shrub zones were compared for a) percent cover and b) density at Site 2 in 2010. There was no significant difference between fertilized plots and vegetation growing along the shrub dripline. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control.

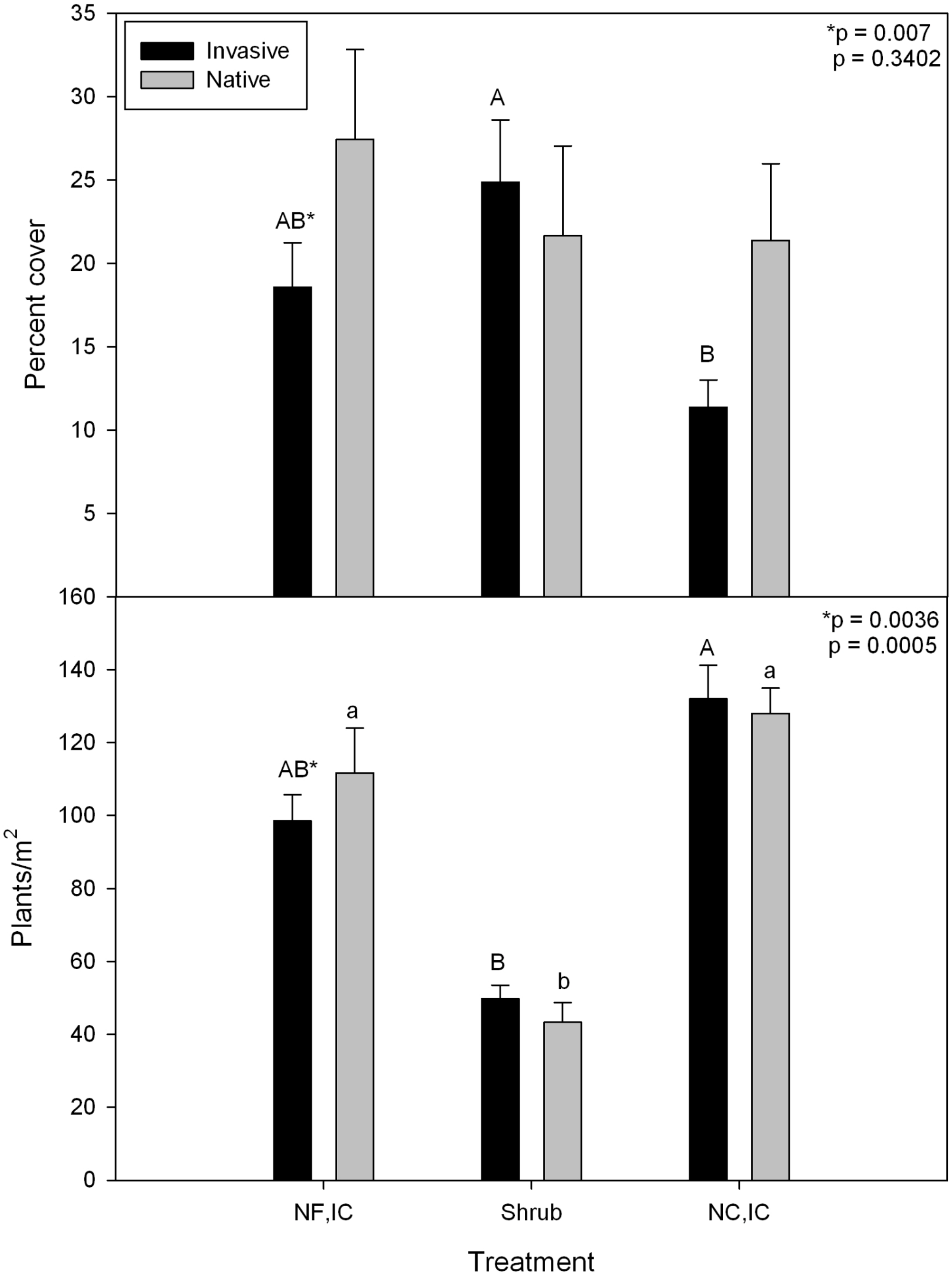


Table 4.6 a & b. Soil nitrogen concentrations [µg/g mean extractable NH_4^+ and NO_3^- (SE)] in response to fertilizer treatments and exotic invasive removal for a) Site 1 and b) Site 2. In 2008, only exotic grass was removed from IR plots. Site 2 was added in 2009, therefore only Site 1 has data for 2008. Significant differences are denoted by an asterisk (*). NF = nitrogen fertilized, NC = nitrogen control, IC = invasive control, IR = invasive removal.

a)

Year	Treatment	Mean (SE)	Significance	p-value
2008	NC,IR	11.5 (0.08)	B	0.0833
	NC,IC	8.3 (0.93)	A	
	NF,IR	16 (0.53)	C	
	NF,IC	25.3 (0.28)	D	
2009	NC,IR	7.4 (1.2)	A	0.0001*
	NC,IC	6.6 (0.66)	A	
	NF,IR	34.8 (4)	B	
	NF,IC	34.6 (3.8)	B	
2010	NC,IR	3.4 (0.26)	A	0.0001*
	NC,IC	4 (0.77)	A	
	NF,IR	43.9 (8.6)	B	
	NF,IC	64.8 (13.2)	B	

b)

Year	Treatment	Mean (SE)	Significance	p-value
2009	NC,IR	7.5 (0.67)	A	0.0001*
	NC,IC	5.6 (0.66)	A	
	NF,IR	33 (7.5)	B	
	NF,IC	20.9 (3.2)	AB	
2010	NC,IR	4.7 (0.67)	B	0.0001*
	NC,IC	3.6 (0.42)	B	
	NF,IR	58.2 (11.7)	A	
	NF,IC	39.5 (6.1)	A	

Table 4.7. Individual species responses to nitrogen fertilization and invasive removal treatments at a) Site 1 and b) Site 2. Significant differences are denoted by an asterisk (*). NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = invasive removal.

a)

Year	Species	Treatment	Percent cover	Significance	p-value
2008	*Filago arizonica*	NC,IR	1.8	A	0.0282*
		NC,IC	1.3	A	
		NF,IR	0.6	A	
		NF,IC	0.6	A	
2009	*Cryptantha angustifolia*	NC,IR	8.7	A	0.0055*
		NC,IC	7.8	A	
		NF,IR	20.3	B	
		NF,IC	13.5	AB	
	Eriastrum diffusum	NC,IR	4.1	A	0.0471*
		NC,IC	4.8	A	
		NF,IR	1.3	A	
		NF,IC	1	A	
	Loeseliastrum schottii	NC,IR	0.61	A	0.0089*
		NC,IC	0.27	A	
		NF,IR	0.18	A	
		NF,IC	0.008	A	
	Pectocarya heterocarpa	NC,IR	3.4	A	0.026*
		NC,IC	2.7	A	
		NF,IR	12.3	A	
		NF,IC	11.3	A	
2010	*Eriastrum diffusum*	NC,IR	3.3	A	0.0061*
		NC,IC	3.1	A	
		NF,IR	1.1	AB	
		NF,IC	0.6	B	
	Pectocarya linearis	NC,IR	0.08	A	0.0224*
		NC,IC	0	A	
		NF,IR	2.8	A	
		NF,IC	0.33	A	

b)

Year	Species	Treatment	Percent cover	Significance	p-value
2009	*Camissonia pallida*	NC,IR	0.19	A	0.0165*
		NC,IC	0.06	A	
		NF,IR	0.05	A	
		NF,IC	0	A	
2010	*Pectocarya recurvata*	NC,IR	13.9	A	0.0177*
		NC,IC	8.42	AB	
		NF,IR	9.5	AB	
		NF,IC	2.6	B	

Table 4.8. Tissue nitrogen concentrations and tissue C:N ratios for plants growing in NF,IC, NC,IC plots, and shrub zones. NF = nitrogen fertilized, NC = nitrogen control, IC = invasive control. Significant differences are denoted with an asterisk (*).

Functional group	Site	Tissue %N	p-value	Significance	C:N (SE)	p-value	Significance
	NF,IC	2.1 (0.2)		A	21.2 (1.54)		A
Invasive	Shrub	1.7 (0.2)	0.2076	A	24.01 (1.96)	0.1552	A
	NC,IC	1.7 (0.2)		A	27 (2.6)		A
	NF,IC	2 (0.1)		A	21.86 (1.43)		A
Native	Shrub	1.9 (0.1)	0.0006*	A	23.01 (1.77)	0.0006*	A
	NC,IC	1.4 (0.06)		B	30.24 (1.11)		B

Table 4.9. Soil nitrogen concentrations [µg/g mean extractable NH_4^+ and NO_3^- (SE)] were compared between NF,IC, NC,IC plots, and shrub zones at Site 2 in 2010. NF = nitrogen fertilized, NC = nitrogen control, IC = invasive control. Significant differences are denoted with an asterisk (*).

Treatment	Mean (SE)	Significance	p-value
NF,IC	39.5 (6.1)	A	0.0002*
Shrub	5.7 (0.33)	B	
NC,IC	3.6 (0.42)	B	

Table 4.10. Native and invasive plot productivity for NF,IC, NC,IC plots, and shrub zones at Site 2. Productivity was analyzed at the plot scale and scaled up to kg ha^{-1}. Standard error is listed in parentheses. NF = nitrogen fertilized, NC = nitrogen control, IC = invasive control. Significant differences are denoted with an asterisk (*).

Functional group	**Site**	**Aboveground N (kg ha^{-1})**	**Significance**	**p-value**	**Biomass (kg ha^{-1})**	**Significance**	**p-value**
	NF,IC	2	A		187.8	A	
Invasive	Shrub	0.87	A	0.3055	141.8	A	< 0.0001*
	NC,IC	0.55	A		23.3	B	
	NF,IC	1.6	A		196.4	A	
Native	Shrub	1.5	A	0.3135	207	A	< 0.0001*
	NC,IC	0.48	A		50.9	B	

Table 4.11. Tissue C:N ratios were compared by functional group and treatment to compare invasive and native nutrient uptake and allocation. NC = nitrogen control, NF = nitrogen fertilized, IC = invasive control, IR = invasive removal.

Site	Year	Treatment	Functional group	C:N (SE)	Significance	H-value	df	p-value
Site 1	2008	NC,IR	Invasive forb	14.99 (1.21)	A	5.79	1	0.0162*
			Native forb	20.21 (1.18)	B			
		NC,IC	Invasive forb	9.47 (1.29)	A	10.54	2	0.0051*
			Invasive grass	14.26 (0.94)	B			
			Native forb	15.29 (0.95)	B			
		NF,IR	Invasive forb	12.03 (0.71)	A	8.56	1	0.0034*
			Native forb	16.88 (1.21)	B			
		NF,IC	Invasive forb	12.59 (1.34)	A	2.16	2	0.3398
			Invasive grass	13.43 (1.36)	A			
			Native forb	14.58 (0.94)	A			
	2010	NC,IC	Invasive	28.16 (1.59)	A	0.017	1	0.8973
			Native forb	27.67 (1.84)	A			
		NF,IC	Invasive	18.39 (0.93)	A	0.69	1	0.4062
			Native forb	20.68 (1.68)	A			
Site 2	2010	NC,IC	Invasive	26.96 (2.56)	A	0.5405	1	0.4622
			Native forb	30.24 (1.12)	A			
		NF,IC	Invasive	21.2 (1.54)	A	0	1	1
			Native forb	21.86 (1.43)	A			

General Conclusions

The research presented here highlights the complex interactions governing the species composition and growth of winter annual communities in the Colorado Desert. Anthropogenic nitrogen deposition and the invasion of exotic annual species are altering ecosystems worldwide and the relatively nutrient-poor deserts of California are particularly susceptible to disturbance. The highly variable, stochastic nature of desert ecosystems may offer native annuals an advantage over exotic invaders that did not evolve under these conditions. However, by altering soil nutrient levels, nitrogen deposition can alleviate some of the difficulties of surviving in California's desert ecosystems (Brooks 2003).

Chapter 1 of this dissertation demonstrated the ability of exotic invasive annual species to overwhelm the soil seed bank, which is a bet-hedging mechanism used by native annual desert species. Although nitrogen fertilization increased the aboveground percent cover of invasive species, there were no differences in the soil seed bank between fertilized and unfertilized plots. This is an alarming result because it highlights the susceptibility of desert soil seed banks to invasion and the idea that, although added nitrogen can increase aboveground percent cover of invasives, elevated soil nitrogen may only act as a conduit for range expansion and may not be not necessary for the degradation of soil seed banks.

In chapter 2, seed germination under multiple soil nitrogen concentrations was shown to be variable among species. However, species identity may be more important than soil nitrogen in determining seed germination rates. This study also shed light on the different germination strategies used by invasive species. *Bromus madritensis* ssp. *rubens*, a prolific invasive grass in high elevation desert communities, demonstrated nearly 100% germination under all nitrogen treatments. However, *Erodium cicutarium* and *Schismus arabicus*, two prolific invaders in the low desert, displayed more conservative germination rates. Both of these species have been shown to have moderate to long-term seed banking abilities (Mayor et al. 1999, Brooks 2000), which points to the different strategies used by these species. Since it is a prolific seeder with high germination rates, *B. madritensis* ssp. *rubens* is more susceptible to drought than *E. cicutarium* and *S. arabicus* due to its inability to form a lasting soil seed bank. This can lead to shifts in the invasive community (Salo 2004, Minnich 2008), as was observed in chapter 4.

A greenhouse project emphasized the potential of *E. cicutarium* to become a dominant invader in desert communities, especially under nitrogen deposition (chapter 3). Although both native annuals and *E. cicutarium* were able to experience the benefits of increased soil nitrogen and water, *E. cicutarium* typically responded more strongly than natives across all nitrogen levels. However, chapter 4 also offered a glimmer of hope by demonstrating that native annuals can coexist and thrive under increased nitrogen when invasive density is low. All of these results taken together reveal the complex dynamics of desert annual communities and may help prioritize conservation and restoration sites.

One of the overarching themes of this research is the heightened ability of exotic invasive annuals to tolerate and even utilize excess nitrogen in desert ecosystems.

Although native annual species can respond positively to nitrogen additions, there appears to be an intermediate threshold at which maximum benefits are attained, unlike invasive species that continue to garner the advantages of increasing soil nitrogen. Furthermore, this research exposes the potential of *E. cicutarium* to become a more dominant invader in the desert than it has been in the past. Due to the susceptibility of invasive grasses to population crashes (Salo 2004, Minnich 2008) and the ability of *E. cicutarium* to maintain soil seed banks and to increase growth and reproductive effort with nitrogen additions (chapters 2, 3, and 4), *E. cicutarium* has the potential to pose a serious long-term threat to desert communities under nitrogen deposition.

The capacity of native annuals to benefit from nitrogen additions and flourish in areas where invasive density is low has important conservation and restoration implications. Further research is needed to determine nitrogen response thresholds for native annuals as well as invasive plant density thresholds under which native species can coexist with invasives. The development of these thresholds could provide valuable insight and help create conservation and restoration prioritization protocols for land managers, for whom invasive species eradication is often impossible. However, the ability of natives to respond positively to nitrogen additions does not eliminate the need for reduction of anthropogenic nitrogen deposition, which is evidenced by the ability of invasives to respond to nitrogen additions, as well.

The invasion of exotic annual species in the desert combined with the eutrophication of desert soils via anthropogenic nitrogen deposition is damaging native ecosystems. The goal of this research was to shed light on some of the mechanisms by which nitrogen deposition leads to the degradation of desert plant communities and the proliferation of invasive species. Assessing the problem from the level of seeds up to field communities provides a more complete picture of the interactions between increased nitrogen, native annuals, and invasive annuals. While this research highlighted the impending threat of *E. cicutarium* as a dominant invader, it also revealed some promising scenarios of drought cycles under which native annuals can maintain their footing.

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