Tree Population Dynamics at a Desert Springs Complex: From Seed to Landscape

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Ecology, Evolution, and Conservation Biology

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ABSTRACT

The cumulative effects of the abiotic and biotic environment on plant distributions are inherently complex due to spatio-temporal variation. The overall objective of this dissertation was to examine the population processes and environmental conditions that control tree distributions at a desert springs complex.

In chapter 1, I examined the efficacy and spatial pattern of coyote dispersal of Prosopis seeds. Analyses showed that digested seeds remained viable and were deposited in environments suitable for germination, but feces were not a suitable seed bed for seedling emergence. Consequently, seed dispersal by coyotes may act as a demographic bottleneck.

In chapter 2, I examined the effects of water availability and salinity on seed germination, seedling emergence, and seedling survival using a series of controlled laboratory and field experiments to identify the fundamental niches of three dominant tree species. Experimental results showed that the effects of water availability and salinity were strong, but varied among species, ontogenetic stages, and experimental conditions. Physiological tolerances to these abiotic factors were lowest during early seedling survival, suggesting another demographic bottleneck.

In chapter 3, I examined the effects of plant interactions along water and salinity gradients on seedling establishment in the context of the stress gradient hypothesis. Results of the field experiment showed that both herbaceous and woody vegetation ameliorated environmental stress, but the net outcome of plant interactions depended on species, ontogenetic stage, and the stress gradient. Facilitative effects were common
during seedling emergence and early seedling survival, but net interactions shifted to competition and became more consistent along stress gradients as seedlings aged.

In chapter 4, I examined spatial variation in the interactions between trees across Ash Meadows. I developed a map of individual trees using object-based classification of multispectral and LiDAR spatial data and examined spatial interactions between trees using local point pattern analysis. Results provided strong evidence that the importance of competition between trees varied spatially in association with water availability and temporally over tree lifetime.

All together, this research illustrates the spatial and temporal complexity inherent in plant-environment interactions depending on species, ontogenetic stage, and the abiotic and biotic environment.
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OVERVIEW

The spatial distribution of plant species in relation to their environment is of fundamental interest in plant ecology. The cumulative effects of abiotic and biotic factors on plant distributions are inherently complex due to spatial and temporal structuring of the environment and plant population processes. Disentangling how abiotic and biotic factors interact to control spatial distributions is difficult, but necessary to understand how plants will respond to environmental change.

The overall objective of this dissertation was to examine the population processes and environmental conditions that control the spatial distribution of trees at Ash Meadows National Wildlife Refuge in the northern Mojave Desert. This desert springs complex has strong gradients in water availability and salinity that are highly associated with the distribution of plant species. Trees and grasses coexist in savanna ecosystems where groundwater is relatively shallow and thus accessible to both life forms. Spatial patterns of trees reflect the cumulative effects of strong variation in environmental conditions and population processes that may influence tree species differently at different life stages. In this dissertation, I examined the influence of demographic, plant-interaction, and environmental constraints on tree populations at Ash Meadows. I specifically focused on the effects of endozoochorous seed dispersal (Chapter 1), the abiotic environment (Chapter 2), and plant interactions (Chapter 3) on seedling establishment, which is the most limiting life stage for trees in this arid environment. I then examined how competition and the environment continue to influence the spatial pattern of mature trees (Chapter 4).
In Chapter 1, I examined whether seed dispersal by coyotes resulted in seedling establishment of *Prosopis glandulosa* and *P. pubescens*. I modeled the spatial pattern of coyote feces at local and landscape scales, finding that coyotes deposited feces containing viable seeds in locations with environmental conditions suitable for establishment. However, laboratory and field germination experiments revealed that feces themselves were not a suitable substrate for seedling emergence. This implies that in the absence of a diplochorous dispersal syndrome where coyotes interact with a secondary disperser, coyotes may be acting as seed predators and limiting *Prosopis* establishment.

In Chapter 2, I examined the effects of water availability and salinity on seedling germination, emergence, and survival to identify the fundamental regeneration niche of each tree species. In arid ecosystems, water and salinity are likely to be the most limiting abiotic factors across a plant’s life, but particularly during seedling establishment. I found that the effects of water availability and salinity on seedling establishment varied between species, ontogenetic stages, and controlled greenhouse versus field experimental conditions. Water availability, which provides both a necessary resource and a source of physiological stress, generally had greater effects on regeneration. There was a significant niche contraction between seedling emergence and survival of young seedlings for all species, suggesting that early seedling survival is the most limiting ontogenetic stage of regeneration. Larger seedlings and mature trees had a broad niche more similar to that of seedling emergence, likely because they were better able to escape physiological stress associated with the soil surface.

In Chapter 3, I examined the effects of plant interactions along water and salinity gradients on seedling establishment in the context of the stress gradient hypothesis. This
hypothesis predicts that net facilitation should be positively associated with abiotic stress, particularly for resource-based stresses like water. I conducted a field experiment at Ash Meadows that examined the effects of understory and overstory vegetation on seedling emergence and survival and on soil conditions along strong gradients in water and salinity stress. Vegetation ameliorated both water and salinity stresses, indicating potential facilitative effects. Results of survival analyses provided mixed support for the stress gradient hypothesis, with the effects of plant interactions along stress gradients varying by species, ontogenetic stage, and the gradient of interest. The response of *P. glandulosa* establishment to plant interactions along the water availability gradient was monotonically positive, conforming to predictions of the stress gradient hypothesis. The response of *F. velutina* establishment to plant interactions along the salinity gradient was generally opposite of that predicted by the stress gradient hypothesis, likely because the ameliorative effects of other vegetation were insufficient to counteract the low salinity tolerance of this species. Net effects of plant interactions shifted from facilitation to competition and became more consistent along stress gradients as seedlings aged.

In Chapter 4, I examined spatial variation in the net interactions between established trees associated with water availability at the landscape scale. I first developed a spatial dataset of individual trees using object-based classification of multispectral and LiDAR spatial data. Classification resulted in successful identification of tree cover and delineation of the majority of trees >2-m tall, with some inaccuracy in delineating individual trees in dense woodlands. I then examined spatial associations between the individual trees using point pattern analysis methods at local (<40 m) scales consistent with the rooting extent of trees. Regularity in the spatial pattern of trees and a
positive relationship between distance and size of nearest neighbors for large trees provided strong evidence for competition. These patterns at local scales were positively associated with tree size and negatively associated with distance to surface water, indicating that the effects of competition accumulate over tree lifetimes and vary with resource availability.

This research significantly improves our understanding of plant-environment interactions in a groundwater-driven savanna. Seed dispersal may act as a first bottleneck in *Prosopis* recruitment if dispersal by coyotes, the main primary disperser, is not followed by secondary dispersal. The early seedling stage also appears to be the crucial bottleneck in desert tree population dynamics, with lower survival and tolerance to environmental stress for young seedlings than either seeds or larger trees. I also found evidence of facilitative interactions for seeds and young seedlings where environmental stress was high, providing a pathway to successful seedling recruitment. Together, these demographic bottlenecks may limit the density of trees and prevent formation of dense woodlands in this savanna environment. Results also showed a significant shift to net competition for larger, established trees consistent with their greater demand for resources. The combined effects of demographic, plant-interaction, and environmental constraints limited opportunity for tree establishment and, following episodic tree establishment, formation of dense patches of adult trees. These constraints on tree populations can result in emergent savanna dynamics absent disturbances such as fire.
CHAPTER 1. COYOTE ENDOZOOCHORY OF PROSOPIS: CONSEQUENCES OF GUT PASSAGE, GERMINATION SUBSTRATE, AND SPATIAL PATTERNS OF DISPERsal

ABSTRACT

Effective endozoochory requires that seeds maintain germinability after gut passage, that there is a suitable substrate for germination, and that animal dispersers deposit seeds in environments suitable for establishment. We sought to determine if coyotes (Canis latrans) are effective dispersers of western honey mesquite (Prosopis glandulosa var. torreyana) and screwbean mesquite (P. pubescens). Mesquites have increased their ranges over the past two centuries in southwestern North America and are among the dominant tree species at Ash Meadows National Wildlife Refuge, Amargosa Valley, NV, USA. We performed a laboratory experiment examining the effects of gut passage on seed germinability, conducted a field experiment comparing emergence from feces and soil, and developed spatial models of the distribution of coyote feces. Gut passage positively affected screwbean mesquite seeds through high rates of removal of seeds from their legumes and of germination, but had limited effect on honey mesquite seeds. However, only two screwbean mesquite seedlings and no honey mesquite seedlings emerged from 81 feces, while many seedlings emerged from soil. Coyotes deposited feces near water and human land use in riparian areas, savannas, and dunes, environments that are likely suitable for establishment. Although feces are an unsuitable substrate for germination, coyote primary dispersal may still contribute to mesquite establishment if seeds from feces are incorporated into the soil seedbank or undergo secondary dispersal. Further research is necessary to determine the potential of these
mechanisms. This study highlights the need to simultaneously consider the effects of gut passage, germination substrate, and spatial patterns of dispersal to determine the effectiveness of endozoochory.

**INTRODUCTION**

Endozoochory, or seed dispersal via ingestion by animals, is a widespread dispersal syndrome that can influence seed germination through gut passage, suitability of feces as a substrate, and the spatial pattern of dispersal. Seeds in large, edible fruits have adaptations for rapid passage through the gut and resistance to digestion (Traveset 1998). Gut passage can scarify seeds, which breaks their physical dormancy (Howe 1980; Gardener et al. 1993; Or and Ward 2003), and can separate seeds from their fruits, which can inhibit germination (Ortega Baes et al. 2001, 2002; Robertson et al. 2006).

Furthermore, gut passage may increase germination rates for seedbanks infested with bruchid beetles due to higher digestibility of beetle-infested seeds and reduced spread of beetles after ingestion (Miller 1994; Or and Ward 2003).

Feces can provide a suitable substrate for germination through increased moisture and nutrient availability (Ocumpaugh et al. 1996) or can inhibit germination and water uptake by seeds (Brown and Archer 1989). Seeds that have not broken dormancy during gut passage may be incorporated into the seedbank or may be moved by secondary dispersers into suitable environments and germinate at a later time (Janzen 1981; Ortega Baes et al. 2001; Vander Wall and Longland 2004). Animals may provide directed dispersal by disproportionately depositing feces in habitat that is suitable for germination (Howe and Smallwood 1982; Chambers and MacMahon 1994) and removing seeds from
distance- or density-related mortality near the mother tree, including that caused by bruchid beetles (Janzen 1970; Howe and Smallwood 1982). Conversely, feces may be deposited in habitat that is unsuitable for seed germination or contain many seeds from the same mother plant, increasing intraspecific competition (Howe 1989; Hulme 2002).

Determining whether endozoochory is advantageous to plant establishment requires examining the cumulative effects of gut passage, deposition in feces, and dispersal patterns on seed germination. Seeds of many plants in the Mimosoideae (Fabaceae) subfamily (e.g., *Prosopis, Acacia*) have physical dormancy requiring scarification and are contained within indehiscent legumes, which require decomposition, ingestion, or other mechanisms to release seeds.

Species of the Mimosoideae are widespread in arid ecosystems and provide crucial ecosystem services, including nitrogen fixation, high quality forage for livestock and wildlife, and wood products and food for humans (Felker 1981; Livingston and Nials 1990). Several of these plants have also increased their ranges and become invasive over the past two centuries, which may be linked to animal dispersal (Brown and Archer 1989; Cox et al. 1993).

Endozoochory is one possible mechanism by which these seeds become germinable and are dispersed across the landscape. Gut passage can have positive, negative, or no effect on seed germination, depending on the Mimosoideae species and the animal disperser (Cox et al. 1993; Campos and Ojeda 1997; Ortega Baes et al. 2002; Kneuper et al. 2003; Silverstein 2005). The suitability of feces as a substrate also differs between plant species and animal dispersers (Kramp et al. 1998; Sánchez de la Vega and Godínez-Alvarez 2010). The ability of animals to disperse *Prosopis* seeds to locations
suitable for germination and establishment after incorporation into the soil seedbank is relatively unknown.

The purpose of this research was to examine the effects of primary dispersal by coyotes (Canis latrans) on germination of western honey mesquite (Prosopis glandulosa var. torreyana [L. Benson] M. Johnson) and screwbean mesquite (P. pubescens Benth.). Honey mesquite seeds can seasonally constitute a substantial portion of coyote feces in the southwestern United States (Meinzer et al. 1975; Ortega 1987; Kramp et al. 1998; Silverstein 2005), suggesting that coyotes may play a significant role as dispersers as do several other animal species (Kneuper et al. 2003). Animal dispersal and germination ecology of screwbean mesquite seeds have not been examined to our knowledge. Coyotes preferentially use habitats based on vegetation structure, water availability, and other landscape factors (Kays et al. 2008; Kozlowski et al. 2008; Atwood et al. 2011). Consequently, deposition of feces is likely non-random as well. Seeds of both mesquite species exhibit physical dormancy, have hard seed coats that require scarification, and are contained within indehiscent legumes. Honey mesquite seeds are also contained within a woody endocarp, while screwbean mesquite seeds are not.

Our question is whether primary dispersal of mesquite by coyotes effectively promotes establishment of mesquite seedlings. Effective dispersal is dependent on germinability after gut passage and deposition of seeds on a substrate and in an environment suitable for establishment; failure of either of these processes indicates that coyotes are not likely to be effective dispersers. We performed a laboratory experiment to compare the effects of gut passage through coyotes on germination to those of mechanical removal from the legume and mechanical/chemical scarification. We
conducted a field experiment to examine seedling emergence from coyote feces and soil substrates in different microhabitats. Finally, we mapped the distribution of coyote feces at Ash Meadows National Wildlife Refuge, Amargosa Valley, NV, to develop spatial models of mesquite seed dispersal by coyotes. Together, these analyses provide a framework to describe the efficacy of coyote endozoochory for mesquite dispersal.

**METHODS**

We collected coyote feces and mesquite legumes at Ash Meadows National Wildlife Refuge, a 9310-ha wetland complex in the Mojave Desert in southern Nevada, USA (36°25′12″N, 116°19′48″W; ca. 670 m a.s.l.). Dominant vegetation varies with water availability and includes: emergent wetlands (*Typha* spp., *Scirpus* spp., and *Eleocharis* spp.) where surface water is present, mesquite bosques at intermediate water availabilities, and desert scrub on dry, upland sites (*Atriplex* spp., *Lycium* spp., and *Larrea tridentata* [DC.] Cov.). Honey mesquite generally occurs on drier sites than screwbean mesquite.

Between September and November 2009, during the season of maximum mesquite seed dispersal, we collected samples of 30-50 legumes per tree from the ground surface beneath 10 to 17 trees from 7 sites for honey mesquite and 9 sites for screwbean mesquite. We walked approximately 80 km along a random path across the refuge, encountering 147 coyote feces and collecting 79.6% (n = 117) of those encountered (Fig. 1). We did not collect feces that were deposited in previous years as evidenced by color or dissolution or that did not have mesquite seeds visible on the exterior. Coyote feces are conspicuous and easily detected in all vegetation types. For each feces, we recorded the
location, substrate type, canopy cover, and distances to water, mature mesquite trees, and roads.

For 30.8% of the feces (n = 36), we classified mesquite seeds by the presence or absence of the endocarp for honey mesquite and exocarp for screwbean mesquite, presence of bruchid beetles (*Algarobius prosopis*) or their exit holes, and damage due to ingestion. We compared the proportion of seeds in each category between species using two sample z-tests. We weighed the proportion of material in each category to estimate the distribution and amount of seed in feces across the landscape. For the remaining 69.2% of the feces (n = 81) used in the subsequent field experiment, we recorded the total weight and visually identified the species of mesquite seeds visible on the surface of the feces.

**Laboratory experiment**

The laboratory experiment was designed to parse the effects of removal from the legume, scarification, and beetle infestation on germination of honey and screwbean mesquite. Treatment factors included: collection substrate (feces or trees and ground), bruchid beetle infestation (present or absent), seed pericarp status (removed or intact), and seed scarification status (scarified or unscarified). The treatments were inherently nested (e.g., seeds cannot be scarified unless removed from their pericarps), resulting in a total of 10 treatment combinations. There were four replicates of 25 seeds for each treatment combination for each species. For seeds collected from trees and the ground, we scarified seeds by mechanically nicking honey mesquite (*Vilela* and *Ravetta* 2001) and by a 30-minute 98% H₂SO₄ bath for screwbean mesquite (*Jackson* et al. 1990).
We tested for seed viability using four replicates of 25 seeds of each species using
tetrazolium staining (Moore 1973). Seeds were removed from their pericarps, scarified,
soaked in deionized water for 24 hours, and placed in Petri dishes on filter paper soaked
with a 1% solution of 2,3,5-triphenyl tetrazolium chloride. Dishes were wrapped in foil
and incubated at 30°C for three hours, at which point staining was evident. Embryos
stained red or pink were considered viable. Mean (±SD) viability proportions were
0.99±0.02 for honey mesquite and 0.97±0.02 for screwbean mesquite.

Seeds were incubated in a dark growth chamber in 100 x 100-mm square plastic
Petri dishes containing 60 g of sand saturated with deionized water at 30°C for 16 hours
and 12°C for eight hours. These correspond to the mean daily maximum and minimum
temperatures in April and May, the beginning of the growing season. We recorded
germination weekly for a minimum of 30 days or until no additional seeds germinated for
seven days. Seeds were considered germinated when the radicle emerged at least 2 mm
from the seed. We analyzed the effects of pre-germination treatment on germination
proportion for each species using one-way ANOVA. Significant differences were
evaluated using Tukey’s test.

Field experiment

We placed the 81 feces that were not dissected back into the field in January 2010
on two transects along water availability gradients defined by changing dominant
vegetation. Along these same two transects and at the same locations, we planted 10
mechanically scarified seeds of each mesquite species 0.5-cm deep. Feces and seed
placement was stratified by canopy cover (under tree canopy or in interspace) and
substrate (bare soil where vegetation was removed, grass, or litter). We expected these factors to affect feces moisture, and thus seed imbibition. We monitored feces and planted seeds for seedling emergence and survival every 1-2 months during the 2010 growing season (March to November). During this monitoring, we collected a surface soil sample to 10-cm depth from within 0.5 m of the seeds for measurement of gravimetric soil water content (GSWC) and electrical conductivity (EC), an indicator of salinity. Together, these provide a measure of water availability. Soil samples were weighed, dried at 105°C for 72 hours, and reweighed to calculate GSWC. Soils were wetted to saturation for measurement of EC.

We compared seedling emergence from feces with emergence from seeds planted nearby in the soil to determine the suitability of feces as a substrate at each location. We then identified conditions necessary for seed germination of each species by comparing the distributions of environmental factors between locations where seeds in feces emerged, planted seeds emerged, and all locations using Pearson’s $\chi^2$ test for categorical factors and student t-tests for continuous water availability measures.

**Spatial analysis of coyote seed dispersal**

We analyzed the spatial pattern of coyote dispersal of mesquite seeds through deposition of feces at local and landscape scales. At local scales, we summarized the proportions of coyote feces deposited on different substrates (bare soil, grass, or litter), under tree canopies versus in interspaces, on or off roads, and near (<3 m) or far from water. We calculated the equivalent proportion of tree, road, and surface water cover within a 10-m belt surrounding the random walking paths using GIS data to determine
null conditions. Feces locations were compared to these null conditions using Pearson’s $\chi^2$ test. There was no equivalent test for substrate composition due to a lack of comparable GIS data.

At the landscape scale, we developed probability maps of coyote dispersal of honey and screwbean mesquite seeds using maximum entropy modeling (Maxent), a machine learning method for presence-only occurrence data (Phillips et al. 2006). Maxent estimates the probability distribution of a species or phenomenon (in this case, coyote feces) that has the largest spread (i.e., maximum entropy) subject to presence-only observations and in relation to a set of “feature” data that can include thresholds, gradients, or categorical environmental data (Phillips et al. 2006). Model gain, an indicator of the probability of occurrence, assesses how closely the model is concentrated around the presence observations in comparison to a uniform distribution. Maxent avoids making assumptions about what is unknown, including the meaning of observed absences, and weights each feature variable according to the complexity it adds to a model to prevent overfitting. Maxent generally performs well compared to other species distribution models (Phillips et al. 2006; Elith and Graham 2009).

We included eight predictor variables related to topography (elevation and slope), habitat (vegetation height, vegetation abundance, generalized vegetation types, and distance to surface water), and human land use (distance to roads and distance to buildings). Elevation and slope were derived from a digital elevation model constructed from 1-ft LiDAR data, and vegetation height was interpreted from the associated LiDAR canopy model (White Horse Associates 2008). Vegetation abundance was estimated by proxy of the soil adjusted vegetation index (SAVI) calculated from 30-m Landsat
Enhanced Thematic Mapper (ETM+) images from July 2009. Generalized vegetation
types (emergent vegetation, riparian forest, mesquite bosque, grassland alkali scrub,
dunes, and desert scrub), surface water, roads, and buildings were derived from photo-
interpretation of true-color 1-m resolution digital orthographs (Sunderman and Weisberg
2012). Surface water and human land use variables were extrapolated across the
landscape using Euclidean distance.

To build our dispersal suitability models (akin to habitat suitability models), we
used Maxent 3.3.3 (Phillips et al. 2006; http://www.cs.princeton.edu/~schapire/maxent/)
using the default settings (regularization multiplier = 1, maximum iterations = 500,
convergence threshold = $10^{-5}$, maximum number of background points = 10,000). We ran
ten replicates in which 80% of feces occurrences were randomly selected as training data,
with the remaining 20% used for model testing. We used the average area under the curve
(AUC) of receiver operating characteristic (ROC) analysis for the 10 replicates as a
measure of predictive performance. We also used jackknife analyses of the model
training gains to assess the importance of each predictor variable.

**RESULTS**

Honey mesquite seeds were present in 71.4% and screwbean mesquite seeds were
present in 51.4% of dissected coyote feces (n = 36). Coyote feces contained large
numbers of mesquite seeds (n = 2784 seeds for honey mesquite and n = 10341 seeds for
screwbean mesquite). Screwbean mesquite seeds were more frequently freed from their
pericarps ($z = -32.19, P < 0.001$) and were less frequently infested by bruchid beetles
than honey mesquite seeds ($z = 8.64, P < 0.001$) (Table 1). No screwbean mesquite seeds
and 12% of honey mesquite seeds exhibited visible damage from coyote ingestion ($z = 35.68, P < 0.001$).

**Laboratory experiment**

Pre-germination treatments had significant effects on germination of both honey ($F_{9,31} = 78.27, P < 0.001$) and screwbean mesquite ($F_{9,31} = 19.11, P < 0.001$). In all cases, beetle-infested seeds failed to germinate (Table 2), so the following results focus on seeds that were not infested by beetles. For honey mesquite, gut passage improved germination rates through both removal from the exocarp (even if the woody pericarp remained) and scarification relative to unscarified seeds within intact endocarps (Table 2; Fig. 2). However, gut passage resulted in significantly lower germination rates than seeds that were manually removed from their endocarps and manually scarified (Table 2; Fig. 2), suggesting loss of seed viability.

In contrast, gut passage appeared to improve germination rates of screwbean mesquite seeds primarily through removal from the pericarp. No seeds germinated from within intact pericarps, regardless of treatment agent (Table 2; Fig. 2). Manual scarification did not result in significantly higher germination rates than unscarified seeds, but did reduce variability (Table 2; Fig. 2). Screwbean mesquite seeds did not experience loss of viability after gut passage, with some replicates experiencing higher germination rates than manually treated seeds (Table 2; Fig. 2). Gut passage also resulted in less variable germination rates compared to unscarified seeds (Fig. 2), indicating a potential role of scarification.
Field experiment

The field experiment suggested that coyote feces provide a poor substrate for mesquite seedling emergence. We observed only two screwbean mesquite seedlings and no honey mesquite seedlings emerge from the 81 coyote feces. Both screwbean mesquite seedlings emerged from feces under the canopies of screwbean mesquite trees where the soil surface was visibly moist in January. The two seedlings emerged in May 2010 from feces within 25 m of each other and survived only through August 2010.

The range of field conditions under which mesquite seeds germinated in soil was substantially greater than the range in which they germinated in feces. Screwbean mesquite seedlings emerged from seeds planted in soil at 44.4% of locations, with no significant difference in emergence based on substrate or canopy cover ($\chi^2 = 5.077, P = 0.079$). Similarly, honey mesquite seedlings emerged from planted seeds at 33.3% of locations, also with no significant difference in emergence based on substrate or canopy cover ($\chi^2 = 1.029, P = 0.598$).

Soils near feces with emergence of screwbean mesquite seedlings had intermediate water content, with GSWC at the start of the growing season in March of ~0.35 g g$^{-1}$ (Fig. 3). Soils where planted screwbean mesquite seeds emerged generally had GSWC between 0.12 and 0.67 g g$^{-1}$, more than the minimum measurement of 0.03 g g$^{-1}$ and less than the maximum measurement of 0.73 g g$^{-1}$ (Fig. 3). Honey mesquite seedlings emerged where seeds were planted across the entire range of GSWC (Fig. 3). Neither screwbean mesquite nor honey mesquite seedlings emerged where EC exceeded 31 dS m$^{-1}$ (Fig. 3).
**Spatial analysis of coyote dispersal**

At local scales, coyotes preferentially deposited feces on roads and near water (Table 3). Of those not located on roads, 12.5% were located on coyote trails. Feces were deposited proportionally under tree canopies and in interspaces (Table 3). The majority of feces were deposited on bare soil, not grass or litter (83.0%, 10.2%, and 6.8%, respectively).

At the landscape scale, the most important predictor of coyote feces presence in the final Maxent model was distance to surface water (52% contribution), with elevation (16.4% contribution), generalized vegetation types (13.2% contribution), distance to buildings (10% contribution), and distance to roads (6.6% contribution) also contributing (Fig. 4). Vegetation abundance, vegetation height, and slope contributed minimally to the final model (Fig. 4). The probability of feces presence decreased dramatically with increasing distance to surface water, with the probability falling below 0.5 for areas over 500 m from surface water (Fig. 5). Feces were more likely to occur in the riparian, savanna, and dunes vegetation types (Fig. 5), all of which are located relatively close to surface water and include mesquite trees as co-dominants. The probability of feces presence was also higher within a narrow 2150 to 2330 m elevation band and closer to human land use (Fig. 5). The Maxent model AUC of 0.859±0.001 for the training data and 0.621±0.071 for the test data substantially exceeded the random prediction of 0.5, indicating good predictive accuracy. Model predictions identified several hotspots as highly suitable for coyote feces deposition (Fig. 6); these areas were located where tree cover is high, suggesting they are also suitable environments for establishment.
DISCUSSION

Our approach provides a framework towards a functional understanding of endozoochory that considers independently the effects of gut passage, germination substrate, and the spatial pattern of seed dispersal. We found positive or neutral effects of gut passage and dispersal of seeds into suitable environments, but that feces were a poor germination substrate. The positive effects of gut passage and the frequency of mesquite seeds in feces suggest coyotes may contribute to mesquite dispersal. Gut passage through coyotes enhanced germination for both honey and screwbean mesquite, primarily through the removal of seeds from indehiscent legumes (Ortega Baes et al. 2001, 2002; Villagra et al. 2002; Robertson et al. 2006). For mesquite and other species with hard-coated seeds, seed liberation appears to be the main benefit of ingestion by many animals, including goats (Ortega Baes et al. 2002; Kneuper et al. 2003), donkeys (Ortega Baes et al. 2002), horses (Janzen 1981; Campos and Ojeda 1997), cattle (Cox et al. 1993; Campos and Ojeda 1997; Kneuper et al. 2003), sheep (Cox et al. 1993; Kneuper et al. 2003), rodents (Campos and Ojeda 1997), foxes (Campos and Ojeda 1997), and bears (Auger et al. 2002).

We found coyote gut passage to be more effective for enhancing germination of screwbean mesquite than honey mesquite. Only 5.2% of honey mesquite seeds were freed from their woody endocarps by coyote ingestion, while 36.9% of screwbean mesquite seeds were freed from their pericarps. Similarly, germination rates after coyote gut passage were substantially higher for screwbean mesquite than honey mesquite (Table 2; Fig. 2). Other studies have found similarly low germination rates of honey mesquite seeds after coyote gut passage (Kramp et al. 1998; Silverstein 2005). Coyote gut passage
also decreased viability of honey mesquite seeds, but not screwbean mesquite seeds. All
together, low rates of seed liberation and germination and decreasing seed viability after
gut passage suggest that coyotes may primarily act as seed predators rather than effective
dispersers of honey mesquite. Conversely, high seed liberation and germination rates
after gut passage suggest that coyotes may be effective dispersers of screwbean mesquite
if seeds are later buried.

In contrast to the positive effects of gut passage, our results suggest that coyote
feces themselves are not suitable for mesquite germination, as also observed by Kramp et
al. (1998). Under field conditions, only two screwbean mesquite seedlings and no honey
mesquite seedlings emerged from feces. The screwbean mesquite seedlings emerging
from feces then died before the end of the growing season. Feces contained abundant
seeds (Table 1), with many seeds remaining visibly ungerminated on the surface at the
end of the growing season (pers. obs.). In comparison, 53.7% of screwbean mesquite
seedlings and 40.9% of honey mesquite seedlings that emerged from soil survived until
the end of the growing season. Seedling emergence was high in 2010 (pers. obs.), likely
due to precipitation that was 52% higher than normal (Amargosa Valley weather station,
Western Regional Climate Center), indicating that successful emergence from feces is
likely a very rare event.

Alternatively, seeds that remain viable and dormant after gut passage could be
incorporated into the seedbank and germinate at a later date. Mesquite seeds have
physical dormancy and can maintain some viability after multiple years in the soil
seedbank, even under conditions suitable for germination (Tschirley and Martin 1960).
Coyotes preferentially deposited feces in environments that could be suitable for tree
establishment if seeds came into contact with a suitable substrate and dormancy was broken. In particular, we found that coyotes disproportionately deposited feces near surface water (e.g., Kays et al. 2008; Atwood et al. 2011), where soils are more likely to be moist and thus promote germination. Coyotes also deposited feces in vegetation types that include mesquite trees, indicating that these environments have been suitable for establishment in the past. For this landscape scale primary dispersal to result in successful establishment, some form of secondary dispersal is likely necessary to incorporate seeds into soil.

Janzen (1981) and Kneuper et al. (2003) suggest that secondary abiotic dispersal may result from fluctuations in environmental conditions, like moisture or temperature, or environmental processes, like erosion or chemical etching, that can decompose woody tissues and move seeds along the soil surface and within the soil profile. However, the efficacy of these abiotic processes for secondary dispersal is unknown and likely to be low. Because seeds must be freed from their woody pericarps for abiotic dispersal to occur and microbial decomposition is unlikely to free seeds of these species (Ortega Baes et al. 2001), animal ingestion by coyotes or other species may be a necessary first step towards germination. Further research is necessary to determine the efficacy of this pathway to germination.

Secondary animal dispersal is the more likely pathway by which viable seeds freed from their legumes could be incorporated into the soil seedbank and deposited in suitable substrates (Villagra et al. 2002; Vander Wall and Longland 2004). In particular, ant or rodent dispersal of seeds from coyote feces or trees to more suitable microsites could lead to high rates of establishment (Vander Wall and Longland 2004; Beck and
Vander Wall 2011). Kangaroo rats are particularly effective dispersers of honey mesquite and the morphologically similar velvet mesquite (*P. velutina*) through their caching of seeds in suitable microsites (Reynolds and Glendening 1949; Reynolds 1954). To our knowledge, no studies have examined rodent dispersal of screwbean mesquite. Seeds dispersed by kangaroo rats are cached in clumps, resulting in emergence of multiple seedlings within a small area (Reynolds and Glendening 1949). However, we did not observe a clumpy distribution of naturally regenerating seedlings at Ash Meadows. If coyotes participate in diplochory with other animal dispersers, an additional benefit of coyote dispersal could be reduced predation from bruchid beetles (Howe and Smallwood 1982; Chambers and MacMahon 1994; Miller 1994; Or and Ward 2003; Rodríguez-Pérez et al. 2011). We observed high rates of beetle predation in coyote feces (Table 1) and found that seeds infested with bruchid beetles were not able to germinate, regardless of ingestion by coyotes. Because beetles are likely to eventually infest all seeds remaining in legumes under trees (Miller 1994; Ortega Baes et al. 2001; Or and Ward 2003), coyote ingestion may reduce seed loss due to beetles. More research is needed to determine if secondary dispersal by ants and rodents of seeds from coyote feces to suitable microsites increases the efficacy of coyote dispersal of mesquite (e.g., Cox et al. 1993; Villagra et al. 2002; Vander Wall and Longland 2004).

**CONCLUSIONS**

To determine the functional effectiveness of endozoochorous seed dispersal mechanisms, it is critically important to consider the effects of gut passage, germination substrate, and the spatial pattern of seed dispersal with respect to environmental
suitability for seedling emergence. Yet few studies of endozoochory have done so. Here, we present methods that link mechanistic experiments on mesquite germination to spatial models of coyote dispersal. As our results demonstrate, positive effects of gut passage on germination are not necessarily indicative of effective animal dispersal because seeds may be deposited in locations where establishment is unlikely. Although coyotes preferentially deposit feces in environments suitable for establishment, coyote feces are not a suitable substrate for germination. Collectively, our results suggest that coyotes may be effective long distance dispersers of seeds away from beetle predation near the mother plant and into suitable environments at the landscape scale. More research is needed to determine if secondary dispersal moves seeds into suitable substrates and microsites for germination.

ACKNOWLEDGMENTS

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**Tables**

**Table 1.** Mean (±SE) counts and proportions of undamaged seeds found in dissected coyote feces classified by the presence of a pericarp enclosing the seed and evidence of beetle damage.

<table>
<thead>
<tr>
<th>Presence of:</th>
<th>Pericarp*</th>
<th>Beetles</th>
<th>Honey mesquite (n = 25)</th>
<th>Screwbean mesquite (n = 18)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Count</td>
<td>Proportion</td>
<td>Count</td>
</tr>
<tr>
<td>Yes</td>
<td>No</td>
<td>60.96±8.04</td>
<td>0.59±0.04</td>
<td>245.78±31.06</td>
</tr>
<tr>
<td>Yes</td>
<td>Yes</td>
<td>48.48±7.08</td>
<td>0.39±0.04</td>
<td>114.78±22.28</td>
</tr>
<tr>
<td>No</td>
<td>No</td>
<td>4.94±1.09</td>
<td>0.05±0.01</td>
<td>139.47±36.92</td>
</tr>
<tr>
<td>No</td>
<td>Yes</td>
<td>4.13±0.74</td>
<td>0.03±0.00</td>
<td>83.82±17.59</td>
</tr>
</tbody>
</table>

*Pericarp refers to the intact endocarp for honey mesquite and intact exocarp for screwbean mesquite.

**Table 2.** Germination proportions (mean±SE) for honey and screwbean mesquite after treatments resulting in the presence or absence of a pericarp and different scarification agents. No seeds infested with beetles germinated. Letters refer to significant differences within columns.

<table>
<thead>
<tr>
<th>Pericarp*</th>
<th>Scarification</th>
<th>Germination proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Honey mesquite</td>
</tr>
<tr>
<td>Present</td>
<td>N/A</td>
<td>0±0</td>
</tr>
<tr>
<td>Present</td>
<td>Coyote</td>
<td>0.09±0.03^ab</td>
</tr>
<tr>
<td>Absent</td>
<td>N/A</td>
<td>0.62±0.11^d</td>
</tr>
<tr>
<td>Absent</td>
<td>Manual</td>
<td>1.00±0.00^c</td>
</tr>
<tr>
<td>Absent</td>
<td>Coyote</td>
<td>0.10±0.04^ab</td>
</tr>
</tbody>
</table>

*Pericarp refers to the intact endocarp for honey mesquite and intact exocarp for screwbean mesquite.
Table 3. Results of Pearson’s $\chi^2$ tests for differences in the proportions of the presence and absence of environmental factors immediately surrounding feces versus in aggregate within 10-m of the random walking path

<table>
<thead>
<tr>
<th>Factor</th>
<th>Proportions</th>
<th>Test statistics</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Feces</td>
<td>Path</td>
<td>$\chi^2$</td>
</tr>
<tr>
<td>Tree canopy</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Present</td>
<td>0.119</td>
<td>0.089</td>
<td>0.635</td>
</tr>
<tr>
<td>Absent</td>
<td>0.881</td>
<td>0.911</td>
<td></td>
</tr>
<tr>
<td>Road</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Present</td>
<td>0.322</td>
<td>0.115</td>
<td>24.678</td>
</tr>
<tr>
<td>Absent</td>
<td>0.678</td>
<td>0.885</td>
<td></td>
</tr>
<tr>
<td>Nearby water</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Present</td>
<td>0.085</td>
<td>0.036</td>
<td>4.064</td>
</tr>
<tr>
<td>Absent</td>
<td>0.915</td>
<td>0.964</td>
<td></td>
</tr>
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</table>
**FIGURES**

**Figure 1.** Feces collection sites and walking paths at Ash Meadows National Wildlife Refuge, Amargosa Valley, NV.
Figure 2. Boxplots of germination proportions for (A) screwbean and (B) honey mesquite given different pre-germination treatments.
Figure 3. Gravimetric soil water contents and soil electrical conductivities of locations with seedling emergence from feces, emergence from planted seeds, and no emergence for (A) screwbean and (B) honey mesquite.
**Figure 4.** Jackknife analysis of environmental predictor importance in relation to total training gain (i.e., quality) for a Maxent model of coyote feces deposition. Black bars show gain in a model using only that predictor variable, grey bars show gain in a model not including that predictor variable, and the hollow bar shows gain in the full model.
Figure 5. Marginal response curves showing how topography, habitat, and human land use variables affect Maxent model predictions.
Figure 6. Predicted probability distribution map for coyote feces deposition. Darker shading represents more suitable areas.
CHAPTER 2. REGENERATION OF THREE DESERT TREE SPECIES IN RELATION TO WATER AND SALINITY STRESS

ABSTRACT

In harsh desert environments, tree species distribution is most strongly limited by the regeneration phase. Identifying the fundamental regeneration niche, which defines abiotic conditions under which seeds germinate and seedlings establish, is crucial to understanding plant spatial patterns, the relative importance of biotic interactions, and the effects of global change factors on plant distributions. In many arid ecosystems, water and salinity are the most limiting abiotic factors affecting plant establishment and persistence. We examined the effects of water and salinity stresses on the fundamental regeneration niche of three dominant tree species at Ash Meadows National Wildlife Refuge, a springs complex in the northern Mojave Desert. We evaluated differences in the effects of water and salinity stresses between life stages and species in controlled laboratory, greenhouse, and field experiments. Water availability and salinity were significantly related to seed germination, seedling emergence, and seedling survival and growth under controlled and field conditions. In general, water stress had a greater effect on regeneration than salinity. There was a significant niche contraction between seedling emergence and survival of young seedlings for all species, indicating that seedling survival was the most limiting ontogenetic stage of regeneration. Larger seedlings and mature trees of all species also had broad niches relative to the young seedling stage. Species differed predictably according to their morphology and physiology in terms of their optimal water and salinity levels. Results point to the importance of examining
species’ niches across ontogenetic stages to understand how environmental conditions structure plant communities.

**INTRODUCTION**

Plant communities are structured along environmental gradients according to the ecophysiological tolerances of individual species (Whittaker and Niering 1965; Weiher and Keddy 1995; Silvertown 2004). While the environmental conditions under which a plant can survive are often quite broad for mature individuals, the regeneration niche, defined by environmental conditions under which there is successful recruitment of seedlings, may be significantly narrower (Grubb 1977; Parrish and Bazzaz 1985; Collins and Good 1987). Plants may be primarily adapted to environmental conditions during regeneration, rather than during maturity, due to high mortality and the strength of selection pressures (Poorter 2007). As individuals develop from seeds to seedlings, age- and size-dependent changes in environmental tolerances can combine with changes in environmental conditions to lead to shifts in the niche of each ontogenetic stage (Parrish and Bazzaz 1985; Donohue 2005; Quero et al. 2008; Donohue et al. 2010). Niche contractions, expansions, and shifts have been observed, depending on the association of traits between ontogenetic stages (Parrish and Bazzaz 1985; Donohue et al. 2010). Seed germination, seedling emergence, and seedling establishment are ontogenetic stages that are particularly sensitive to environmental conditions and particularly vulnerable to abiotic stress (Schupp 1995; Weiher and Keddy 1995; Kitajima and Fenner 2000). Consequently, regeneration can be a significant bottleneck for population dynamics and a strong influence on plant community structure (Grubb 1977; Parrish and Bazzaz 1985).
Both abiotic and biotic environmental conditions limit regeneration, but distinguishing between the two is difficult because abiotic conditions can be modified by neighboring plants. In turn, the net outcome of competitive interactions is affected by the relative intensity of stress experienced by species under a set of environmental conditions. Direct experimentation is one method through which limitation due to physiological tolerances to abiotic conditions (i.e., the fundamental niche) can be separated from limitation related to biotic interactions. Here, we focus on the fundamental niche across ontogenetic stages in regeneration, excluding the effects of biotic interactions and other ecological processes, to provide a solid foundation from which to explore the role of biotic interactions in species distributions (Chapter 3). This approach also provides greater confidence in extrapolating to novel conditions, including climate change and invasive species.

In arid ecosystems, water availability and salinity are the most likely abiotic factors to limit species distributions (Noy-Meir 1973; Ungar 1991; Bertness et al. 1992). There is generally a strong relationship between physiological tolerance to drought and the distribution of plant species along gradients in water deficit (Pockman and Sperry 2000). Soil water availability and salinity fluctuate within and across growing seasons (Noy-Meir 1973; Knapp and Smith 2001). For phreatophytes, drought stress is likely to be higher for seeds and seedlings relying completely on soil water rather than for mature plants that have roots reaching the water table and can use both soil and groundwater (Snyder et al. 1998; Snyder and Williams 2000; McLendon et al. 2008). Because evapotranspiration concentrates salts at the soil surface, salinity stress is likely to be higher for seeds and seedlings as well.
For many desert species, germination is often timed to coincide with seasonally increased moisture availability and reduced surface salinity (Ungar 1978). Alternatively, exposure to saline conditions and subsequent immersion in low salinity water can lead to enhanced germination (i.e., osmotic priming) or similar germination (i.e., osmotic recovery) relative to germination in low salinity water (Ungar 1978; Woodell 1985; Dodd and Donovan 1999). Osmotic recovery is often associated with a greater salinity tolerance of seeds than actively growing plants, which may lead to low regeneration rates because seedlings cannot survive under the same conditions in which seeds germinate (Ungar 1982). Because seeds rely on their resource reserves, they may be less sensitive to environmental fluctuations than seedlings (Kitajima and Fenner 2000).

The responses of plants to water and salt stresses are complex due to interactions between temporal changes in stress factors and plant physiological mechanisms of stress tolerance. Both stresses include an osmotic effect, while the effects of salinity also includes ionic imbalance and toxicity (Munns 2002). In seeds, water uptake into the apoplast is inhibited by low water potential gradients, while transfer across cell membranes is further inhibited by salt accumulation in the cytoplasm (Hegarty 1978). In seedlings, water and salt stress results in metabolic and hormonal disruptions to growth, while salt stress also disrupts homeostasis and ion distribution in the cell (Munns 2002). Physiological mechanisms of tolerance to persistent water and salt stresses include accumulation of solutes, osmotic adjustment, and reactive oxygen species detoxification (Munns and Tester 2008). To maintain ion homeostasis within cells, salt ions are also actively excluded from plant roots and cytoplasm or sequestered in vacuoles (Munns 2002). Although drought may be more common across the growing season in arid
ecosystems, flooding stress and the associated anaerobic conditions may also seasonally limit root respiration and plant growth in desert wetlands (Kozlowski 1997).

Here, we focus on identifying the effects of water and salinity on the fundamental regeneration niches of three dominant tree species at a springs complex in the Mojave Desert. We examine the soil conditions under which seed germination, seedling emergence, and seedling survival occur as well as those in which trees of each species have naturally established. Specifically, we ask: (1) how do the effects of water and salinity stress differ? And, (2) how does the relationship between regeneration and water and salinity stresses vary among ontogenetic stages, species, and under controlled laboratory and greenhouse conditions versus field conditions? To examine these questions, we conducted controlled laboratory and greenhouse experiments on seed germination and seedling survival under factorial combinations of water and salinity levels to isolate the effects of these stresses on regeneration. We also carried out a field experiment examining seedling emergence and survival from planted seeds and seedlings along water stress gradients.

METHODS

Study area

Ash Meadows National Wildlife Refuge is a 9310-ha wetland complex located in the northern Mojave Desert in Amargosa Valley, NV (36°25′12″N, 116°19′48″W; ca. 670 m a.s.l.). Average temperatures range from highs of 40°C in summer to lows of -1°C in winter, with average annual precipitation of 10 cm. Aridisols are the dominant soil order in upland areas and younger Entisols and Inceptisols are dominant where there are
alluvial deposits. Over 30 springs and seeps discharge 16,500 to 17,500 ac-ft yr\(^{-1}\) of groundwater (Otis Bay and Stevens Ecological Consulting 2006), leading to spatial gradients in water availability associated with depth to groundwater and distance to surface water. Shallow groundwater is associated with accumulation of salts on the soil surface, with common salt forms including halite (NaCl), thenardite (Na\(_2\)SO\(_4\)), and trona (Na\(_3\)H(CO\(_3\))\(_2\)\(\cdot\)2H\(_2\)O) (George Breit, pers. comm.). In areas with shallow groundwater, salt deposits form on the soil surface. Dominant vegetation varies along these gradients from emergent wetlands to grasslands to desert scrub. The spatial distributions of the dominant tree species overlap, but generally place \(P.\) glandulosa on drier sites, \(P.\) pubescens on intermediate sites, and \(F.\) velutina on wetter sites.

**Seed collection, testing, and pre-treatment**

Seeds were collected from 10 to 30 trees per species that were scattered throughout Ash Meadows during the dominant seed dispersal period for each species (September – November). Seeds were collected in 2008 for the greenhouse experiment and to grow seedlings for the field experiment. Seeds were collected in 2009 for the laboratory germination experiment and for direct sowing in the field experiment. We tested for seed viability using four replicates of 25 seeds of each species in 2008 using tetrazolium staining (Moore 1973). Seeds were removed from their fruits and \(Prosopis\) seeds were mechanically scarified to allow penetration of the tetrazolium into the seed tissue. Seeds were then soaked in deionized water for 24 hours and placed in Petri dishes on filter paper soaked with a 1% solution of 2,3,5-triphenyl tetrazolium chloride. Dishes were wrapped in foil and incubated at 30°C for three hours, at which point staining was
evident. Embryos stained red or pink were considered viable. Mean (±SD) viability proportions of 0.40±0.10 for *F. velutina*, 0.98±0.02 for *P. pubescens*, and 0.99±0.02 for *P. glandulosa* were used to calibrate the number of seeds used in each experiment.

To ensure germination, seeds were pre-treated before all experiments. *Prosopis* seeds were removed from their indehiscent legumes to allow germination (Chapter 1). Seeds were pre-treated to break dormancy, with *F. velutina* seeds cold-wet stratified for 60 days at 7°C (except for those directly sown in the field experiment), *P. glandulosa* seeds scarified by nicking (Vilela and Ravetta 2001), and *P. pubescens* seeds scarified using a 98% H$_2$SO$_4$ bath for 30 minutes (Jackson et al. 1990).

**Laboratory germination experiment**

The germination experiment isolated the effects of soil osmotic water potential ($\Psi_s$) and salt toxicity on germination of *F. velutina*, *P. pubescens*, and *P. glandulosa*. Treatments included six water potentials ($\Psi_s = 0, -0.5, -1, -1.5, -2, and -3$ MPa) formulated using two osmotic agents (NaCl and polyethylene glycol, m.w. 8000 [PEG]). Because PEG is metabolically inactive, differences in the effects of the isosmotic solutions differentiate the osmotic and toxic effects of NaCl. If NaCl has only an osmotic effect, germination responses to both solutions should be similar. Salt treatment solutions were formulated by adding NaCl to deionized water in accordance with Van’t Hoff’s equation at 30°C (Lang 1967). Salt solution concentrations for treatments were 0, 99.2, 198.4, 297.6, 396.7, and 595.1 mol m$^{-3}$, and ECs were 0, 9.1, 18.1, 27.2, 36.3, and 54.4 dS m$^{-1}$, respectively. Isotonic polyethylene glycol (m.w. 8000) treatment solutions were formulated by adding PEG to deionized water at 30°C (Michel 1983). The maximum
water potential exceeds those of previous germination experiments using similar *Prosopis* species (Jackson et al. 1990; Catalan et al. 1994; Cony and Trione 1998) and exceeds 85% of water potentials and salinities measured near trees at Ash Meadows.

Four replicates of 25 pre-treated seeds of each *Prosopis* species and eight replicates of 25 pre-treated seeds of *F. velutina* were incubated in 100 x 100-m square plastic Petri dishes containing 60 g of sand saturated with the osmotic solutions. Water potentials of the final NaCl and PEG solutions in saturated sand were not significantly different from each other or from the target water potentials ($P \leq 0.05$ from paired t-tests). We maintained saturated conditions at the desired osmotic potentials by applying deionized water twice weekly to replace losses through evapotranspiration. Seeds were incubated in a dark growth chamber at 30°C for 16 hours and 12°C for eight hours each day to reflect the mean daily maximum and minimum temperatures in April and May, the beginning of the growing season. Germination was recorded twice weekly for 30 days and then weekly until no additional seeds germinated for seven days. Seeds were considered germinated when the radicle emerged at least 2 mm from the seed. Seeds with fungal infections were removed from the experiment. We tested for osmotic recovery effects at the end of the active germination period by returning seeds to deionized water treatments for an additional 30 days or until no additional seeds germinated for seven days.

We analyzed germination proportion for each species using ANOVA models including treatment water potential, osmotic agent, and their interaction. Significant differences were evaluated using Tukey’s test. We analyzed timing of seed germination using survival analysis, modeling ‘germination’ in place of ‘survival’ (Onofri et al.)
In this framework, the probability of germination measures the proportion of individuals that may still emerge at a later date, and thus decreases as more seeds germinate (Onofri et al. 2010). Germination data were right censored because some seeds did not germinate during the course of the experiment. Data were also interval censored because we only knew the 3–4 day interval in which seeds germinated. We constructed emergence functions for each species in each plot using nonparametric maximum likelihood estimates of Kaplan-Meier curves for interval censored data. Survival functions were compared among treatments using a log-rank test reformulated as a linear rank test. Survival analyses were performed using packages ‘interval’ (ver. 1.0-1.2) and ‘coin’ (ver. 1.0-22) in the R statistical environment (ver. 3.0.0; R Core Development Team 2013).

We evaluated osmotic recovery as the increase in germination proportion after immersion in deionized water, indicating recovery from a physiological dormancy induced by high salinity (Woodell 1985). We evaluated osmotic priming by comparing the total germination proportion of the treatment to that under the deionized water treatment, with a higher germination proportion indicating a priming effect. Only dishes with seeds that remained ungerminated at the end of the treatment portion of the experiment were included, causing small sample sizes and incomplete replication for both *Prosopis* species. In particular, high germination proportions of *P. glandulosa* under all NaCl treatments resulted in n = 0.
Greenhouse experiment

The greenhouse experiment examined the interactive effects of soil water availability and salinity on seedling survival and growth over four months. Factorial combinations of five depths to water (10, 16, 23, 30, and 40 cm below the soil surface) and seven levels of salinity (50, 100, 150, 200, 275, 400, and 700 mol m$^{-3}$) were applied to seedlings of *F. velutina*, *P. pubescens*, and *P. glandulosa*. Sixteen replicates of each of the 35 treatment combinations for each species were planted in 0.41-m deep pots (TPOT2, Stuewe & Sons, Tangent, OR) filled with topsoil and submerged in treatment basins in a greenhouse at the University of Nevada, Reno. Not all seeds germinated, so sample sizes were uneven across treatments and species (n = 8.9±1.3 across treatments for *F. velutina*, n = 11.8±2.2 across treatments for *P. pubescens*, and n = 13.0±0.9 across treatments for *P. glandulosa*). During the first two weeks of March 2009, three (*P. glandulosa* and *P. pubescens*) or five (*F. velutina*) pre-treated seeds were planted at 0.5-cm depth in each pot. Pots were watered daily with fresh water until at least one seedling had a true leaf, at which point treatment began. Seedlings were thinned to one plant per pot two weeks after the initial salt application. Seedlings were grown under natural light conditions with no fertilization and a climate controlled daily maximum temperature of 40°C and nightly minimum temperature of 18°C, the mean daily maximum and minimum temperatures at Ash Meadows over the growing season. Treatment basins were refilled weekly to the proper water level using water at salinity equal to that of spring water at Ash Meadows (2 mol Na m$^{-3}$) (George Breit, pers. comm.). Because greenhouse conditions and treatments resulted in different soil moistures and salinities, we measured volumetric soil water content (VSWC) and EC monthly in the top 5 cm of soil using a 5-
TE sensor and ProCheck datalogger (Decagon Devices, Pullman, WA). The five water levels resulted in surface soil VSWC ranging from 0.052 to 1.00. The seven salinity levels led to surface soil EC ranging from 0.1 dS m\(^{-1}\) to 58 dS m\(^{-1}\). The maximum recorded change in EC was 2 dS m\(^{-1}\) month\(^{-1}\), which occurred in the shallowest depth to water (10 cm below the soil surface) at the highest salinity level (700 mol m\(^{-3}\)). A fungus gnat infestation occurred in May and was controlled within a month by application of *Hypoaspis miles* (a predatory mite) and *Bacillus thuringiensis ssp. israelensis* (a microbial insecticide) in conjunction with use of flypaper. Every other week, we measured height and number of photosynthesizing leaves as measures of growth and recorded seedling mortality. At the end of the experiment in July, we harvested up to a maximum of three remaining seedlings of each species in each treatment combination and excavated the roots. We measured aboveground height and length of the main tap root.

We used the seedling mortality records to analyze the differences in seedling survival among water stress treatments and species. Survival data were right- and interval-censored, with mean (±SD) intervals of 13.1±4.5 days, but ranging from 2 to 23 days, between measurements. Survival functions for each treatment were calculated using nonparametric maximum likelihood estimates of Kaplan-Meier curves for interval censored data and compared among treatments using a log-rank test reformulated as a linear rank test.

We tested for water stress effects on height growth and leaf number using linear mixed models with depth to water treatment, salinity treatment, time since planting, and their interactions as fixed effects and individual seedlings as a random effect. Because
data were unbalanced due to unequal sample sizes and survival across treatments, we estimated significance of model parameters by comparisons to a probability distribution obtained by 10,000 Markov Chain Monte Carlo (MCMC) simulations. Mixed effects models were fit using package ‘lme4’ (ver. 0.999999-2) in the R statistical environment.

We tested for differences in root length and root: shoot ratio at the end of the experiment using ANOVA models including depth to water treatment, salinity treatment, species, and their interactions. Significant differences were evaluated using Tukey’s test.

**Field experiment**

We identified two sites with strong gradients in soil water availability and located two transects parallel to the gradient within each site. We used changes in plant species composition along the gradient to define zones of apparent water availability. Within each zone, we subjectively located two representative plots (n = 47) within 10 m of the transect that were not under tree canopies and up to two plots within 25 m of the transect under tree canopies of each species (n = 6 for *P. glandulosa*, n = 17 for *P. pubescens*, and n = 21 for *F. velutina*). Plots in open areas contained six 2 x 1-m subplots; we randomly selected half of the subplots for removal of all understory vegetation and litter by hand and randomly assigned one intact and one cleared subplot to each species. Here, we focus on the subplots where all understory vegetation and litter was removed in order to better isolate the effects of water stress (n = 47).

We planted a dormant seedling in the center of each subplot in January or February 2010. All *Prosopis* seedlings and 62% of *F. velutina* seedlings were grown in 0.41-m deep pots (TPOT2, Stuewe & Sons, Tangent, OR) in the greenhouses at
University of Nevada – Reno from March to August 2009 and then hardened outdoors until planting. The remaining *F. velutina* seedlings were grown at College of Southern Nevada (Henderson, NV), in 17.2-cm deep garden pots from March 2007 to January 2009. We also planted 10 (*Prosopis*) or 50 (*F. velutina*) pre-treated seeds (see collection and pre-treating procedures above) at standardized positions within each treatment subplot. Seeds were buried shallowly at 0.5-cm depth to improve the probability of the radicle penetrating the soil. We provided no supplemental water to seeds or seedlings.

Monitoring occurred every 1−2 months during the growing season (March to October) in 2010 and 2011 and in May 2012. Seedling emergence was only monitored during the first growing season. For each species, we corrected the number of seedlings that emerged from planted seeds by subtracting counts of seedlings that emerged from subplots without planted seeds. We recorded seedling survival and size (height, stem diameter at the root crown, and number of photosynthetically active leaves) for seedlings that emerged from planted seeds and for seedlings that were grown in greenhouses and planted in the field. Seedlings that emerged from planted seeds reached a maximum age of 2 years, while those that were planted into the field were able to reach a maximum of 3−4 years by the end of the experiment. After taking relevant measurements, we collected surface soil samples from 0 to 10-cm depth and then removed vegetation and litter to maintain treatments. Soil samples were weighed, dried at 105°C for 72 hours, and reweighed to calculate gravimetric soil water content and bulk density. Soils were wetted to saturation using deionized water to determine porosity. We calculated VSWC, air-filled porosity, and degree of saturation from these measurements. Saturated pastes were used to measure EC and pH. We examined relationships among soil measurements,
location, and sampling time using linear mixed models with transect, standardized
distance along the transect, measurement month, and measurement year as fixed effects
and plot as a random effect. We estimated significance of model parameters by
comparisons to a probability distribution obtained by 10,000 MCMC simulations.

We analyzed timing of seedling emergence for the 2010 growing season using
survival analysis, modeling ‘emergence’ in place of ‘survival’ (Onofri et al. 2010). In this
framework, the probability of emergence measures the proportion of individuals that may
still emerge at a later date, and thus decreases as more seedlings emerge (Onofri et al.
2010). Emergence data were interval censored, with a mean (±SD) interval of 39.0±18.0
days and intervals ranging from 21 to 83 days during the 2010 growing season. We
constructed emergence functions for each species in each plot using parametric estimates
of Kaplan-Meier curves for interval censored data. The timing of emergence events for
each species was modeled via parametric Accelerated Failure Time (AFT) regression
using package ‘survival’ (ver. 2.37-4) in the R statistical environment. Accelerated
Failure Time regression models how predictor variables are associated with slower or
faster times to emergence. We used a frailty modeling approach (akin to a mixed model),
in which plots defined clusters (akin to a random effect). The AFT model described the
distribution of seedling emergence dates using the Weibull function, in which the
mortality rate is proportional to a power of time; AFT regression using the Weibull
function is therefore equivalent to a proportional hazards model. For each species, we
constructed models including all possible sets of soil predictor variables, including the
interaction between VSWC and EC. Models were ranked using AICc, a second order
form of Akaike’s Information Criterion appropriate for small sample sizes. Coefficients
and 95% confidence intervals (CI) for all model parameters were estimated using
modeling averaging based on Akaike weights of models with ΔAICc < 4 compared to the
minimum model AICc. We calculated time ratios, which describe the expansion or
contraction in time to an event (e.g., emergence or death) that is attributable to a
parameter, by exponentiating model averaged coefficients. A time ratio greater than one
indicates an increase in time to an event, while a time ratio less than one indicates a
decrease in time to an event.

We analyzed timing of survival of seedlings that emerged from planted seeds and
those that were planted in the field using AFT regression and model averaging in the
same fashion as the analysis of timing of emergence. In this case, survival data for March
2010 to May 2012 were interval and right censored, with a mean (±SD) interval of
63.69±74.77 days and intervals ranging from 21 to 305 days due to variation in sampling
intensity across seasons and years. We tested for soil effects on height and stem diameter
using linear mixed models using combinations of all soil variables and the interaction
between VSWC and EC as fixed effects and individual seedlings and time nested within
individual seedlings as random effects. Linear mixed effects models were ranked using
AICc and parameter effect sizes were estimated based on model averaging of Akaike
weights of models with ΔAICc < 4 compared to the minimum model AICc.

RESULTS

Germination

Germination rates differed between species, with *F. velutina* having a
substantially lower germination proportion and slower germination than either *Prosopis*
species (Fig. 1). Water potential, osmotic agent, and their interaction were highly significant for germination proportion of seeds of all species (Table 1). For all species, germination proportion decreased with a decrease in water potential in both NaCl and PEG solutions, but the inhibition was greater in PEG (Fig. 1; Table 2).

Germination occurred from days 2 to 31 for *P. glandulosa* and *P. pubescens* and days 13 to 100 for *F. velutina*. Timing of germination for all species was also significantly related to water potential and osmotic agent, with faster time to germination at lower water potentials and with exposure to NaCl (Fig. 2; Table 2).

We found evidence of osmotic recovery in all species, with the greatest recovery at the highest treatment water potentials (Fig. 1). Exposure to PEG resulted in substantially lower recovery than exposure to NaCl for *F. velutina* and moderately lower recovery for *P. pubescens* (Fig. 1). On average, the total germination proportion including recovery was approximately 60% of the germination proportion under the $\Psi_s = 0$ MPa (deionized water) treatment, indicating a persistent negative effect of exposure to low water potentials (Fig. 1). The exception was *F. velutina* seeds exposed to the $\Psi_s = -0.5$ MPa treatment using NaCl, which had a higher total germination percentage than that under $\Psi_s = 0$ MPa treatment, indicating osmotic priming (Fig. 1).

**Greenhouse seedling survival and growth**

Seedling survival to the end of the greenhouse experiment (4 months) varied between species, with mean survival rates (±SD) across water stress treatments of $0.94±0.08$ for *P. glandulosa*, $0.90±0.11$ for *P. pubescens*, and $0.31±0.24$ for *F. velutina*. Survival was higher at salinities above 50 mol m$^{-3}$ and at intermediate depths to water
(16.51 to 30.48 cm deep) for *P. glandulosa* and *P. pubescens* (Fig. 3). Greater survival of *F. velutina* was associated with intermediate depths to water, but lower salinities (Fig. 3).

The effects of water stress treatments on seedling survival time also differed between species. Survival functions did not differ between depth to water and salinity treatments for *P. glandulosa* ($\chi^2 = 6.17$, df = 34, $P = 1$) or *P. pubescens* ($\chi^2 = 5.73$, df = 34, $P = 1$) and the probability of survival for both *Prosopis* species decreased linearly over time.

In contrast, survival time differed significantly between water stress treatments for *F. velutina* ($\chi^2 = 63.15$, df = 34, $P = 0.002$). The significant interaction between depth to water and salinity treatments manifested as higher survival probabilities for seedlings with deeper water tables at higher salinities (Fig. 4). Differences between survival functions were primarily driven by salinity levels, with seedlings at lower salinities having higher survival probabilities and longer survival times (Fig. 4). The logrank test for differences between salinity treatments after stratifying for depth to water treatments was highly significant ($\chi^2 = 41.86$, df = 6, $P < 0.001$), while the converse test for differences between depth to water treatments was not ($\chi^2 = 6.54$, df = 6, $P = 0.162$).

Depth to water and salinity treatments had significant effects on seedling growth of all species. The interaction between depth to water and salinity significantly affected the intercept and slope (growth rate) of models of seedling height and leaf number, excepting the intercept of leaf number for *P. glandulosa* (Table 3). Taller seedlings of all species were found in treatments with shallower depths to water, with maximum height occurring at 10-cm depth to water and 50 mol m$^{-3}$ salinity for *P. glandulosa* and *F. velutina* and at 6-cm depth to water and 150 mol m$^{-3}$ for *P. pubescens* (Fig. 5). The
salinity treatment with the highest growth rate differed with depth to water and between species. In treatments with deeper depths to water, salinity had little consistent effect on height growth (Fig. 5). At the shallowest depth to water (10 cm), maximal height growth occurred in the lowest salinity treatment (Fig. 5). At the 16-cm depth to water, maximal growth occurred at intermediate salinities of 150 to 200 mol m$^{-3}$ (Fig. 5). Leaf number followed a similar pattern (Fig. 1 in Appendix A). At the end of the experiment depth to water treatment was significantly related to seedling root length ($F = 42.10$, df = 4, $P < 0.001$) and root: shoot ratio ($F = 7.84$, df = 4, $P < 0.001$), with longer roots occurring in treatments with shallower depths to water and a larger root: shoot ratio occurring in treatments with the deepest water depth (Fig. 6).

**Field experiment**

*Soil conditions*

Transects captured significant variation in all soil variables, with ranges of VSWC and EC comparable to those in the laboratory and greenhouse experiments (Table 4; Fig. 7). Unlike the laboratory and greenhouse experiments, there were no field plots that combined both high VSWC and high EC. These water stress variables were significantly related to transect and standardized distance along the transect (Table A2 in Appendix A), and VSWC was also significantly affected by measurement date (Fig. 8; Table A2 in Appendix A). VSWC tended to be highest at the start of the growing season, decreased during the higher temperatures of summer, and increased again in the fall (Fig. 8). Monsoonal rainfall was the source of the higher VSWC recorded in summer 2011 (Fig. 8).
Established trees

Established trees of each species were present along all but transect D at site 2, with 6 *P. glandulosa*, 17 *P. pubescens*, and 21 *F. velutina* trees. Only *F. velutina* trees were present in areas with VSWC > 0.23, and there was a mixture of all species at lower VSWC across the full range of EC (Fig. 9). Established *P. glandulosa* trees were uniformly distributed in relation to VSWC and EC, and had mean (±SD) height of 3.60±3.67 m, canopy area of 37.85±19.67 m², and dead proportion of the canopy of 31.67±16.31. The density of established *P. pubescens* was higher at VSWC between 0.1 and 0.2 (Fig. 9), with mean (±SD) height of 3.66±1.68 m, canopy area of 52.21±64.98 m², and dead percentage of the canopy of 38.82±26.39%. The density of established *F. velutina* trees was higher at VSWC > 0.2 and EC < 11 dS m⁻¹ (Fig. 9). Trees located in these areas of higher VSWC had mean (±SD) height of 5.29±1.69 m, canopy area of 40.53±28.43 m², and dead proportion of the canopy of 0.025±0.038. In comparison, trees located in areas with lower VSWC were larger and more variable in size (mean±SD of 7.29±6.97 m for height and 181.85±262.43 m² for canopy area) and had a larger dead proportion of canopy (0.072±0.11).

Seedling emergence

Seedling emergence of all species occurred from the seedling treatment across the entire growing season, with peak emergence occurring between April and June (Fig. 10). We observed background natural emergence of one *P. glandulosa* seedling, one *P. pubescens* seedling, and 92 *F. velutina* seedlings in 10 subplots without planted seeds. Seedling emergence from planted seeds occurred in 12 plots for *P. glandulosa* (mean±SD...
of 2.1±1.1 seedlings plot\(^{-1}\)), 14 plots for *P. pubescens* (2.7±2.3 seedlings plot\(^{-1}\)), and 22 plots for *F. velutina* (9.1±11.1 seedlings plot\(^{-1}\)). The subplots with background *F. velutina* emergence were located within 5 m of mature female *F. velutina* trees where VSWC > 0.17 and EC < 12 dS m\(^{-1}\).

Seedling emergence of all species was related to soil water content and salinity (Figs. 11–13). Emergence of *P. glandulosa* seedlings occurred where EC < 48 dS m\(^{-1}\) and at VSWC ranging from 0.03 to 0.54 (Fig. 11). Emergence of *P. pubescens* seedlings occurred where EC < 28 dS m\(^{-1}\) and was concentrated at VSWC between 0.1 to 0.4 (Fig. 12). Emergence of *F. velutina* seedlings occurred in similar locations to that of *P. pubescens*: where EC < 36 dS m\(^{-1}\) and 0.1 ≤ VSWC ≤ 0.4 (Fig. 13).

Timing of seedling emergence of all species was related to VSWC, EC, and all other soil variables (Table 5). Model coefficients were similar across all species, although confidence intervals differed (Table 5). The interaction between VSWC and EC led to slower time to emergence at VSWC < 0.33 and faster time to emergence with increases in VSWC, with larger effects at higher EC (Fig. 14). Increases in bulk density significantly prolonged time to emergence for all species, as did increases in air-filled porosity for *F. velutina*. Increases in soil pH, porosity, and degree of saturation led to significantly shorter times to emergence (Table 5).

*Emergent seedling survival and growth*

Of the seedlings that emerged, two *P. glandulosa*, zero *P. pubescens*, and four *F. velutina* seedlings survived until the end of the experiment. Seedling death primarily occurred during the growing season for *P. glandulosa* and occurred relatively evenly
throughout the year for *P. pubescens* and *F. velutina*. According to the averaged AFT regression models, survival of emergent seedlings was significantly related to the interaction between VSWC and EC for *P. glandulosa* and *P. pubescens* and to each variable additively for *F. velutina* (Table 6). For both *Prosopis* species, emergent seedlings that survived to the end of the experiment occurred in plots with intermediate VSWC and low EC, the ranges of which were substantially narrower than those under which seedlings emerged (Fig. 9). For *F. velutina*, emergent seedlings that survived to the end of the experiment were located in plots with higher average VSWC and lower average EC than those of all plots or plots where seedlings had emerged (Fig. 9). Survival time of *P. pubescens* seedlings was also positively related to soil bulk density and pH (Table 6). For *F. velutina*, survival time was also positively associated with air-filled porosity and negatively associated with bulk density and porosity (Table 6).

Height and stem diameter growth of emergent seedlings of *P. glandulosa* during the first growing season significantly exceeded growth of *P. pubescens* or *F. velutina* (Fig. 16). In contrast to the relationships found for survival time, mixed effects models indicated that height and stem diameter growth of emergent seedlings of *P. glandulosa* and *P. pubescens* were not related to VSWC or EC (Table 7). However, height and stem diameter growth of *P. glandulosa* emergent seedlings were positively related to air-filled porosity, and stem diameter growth of *P. pubescens* emergent seedlings was positively related to bulk density (Table 7). For emergent *F. velutina* seedlings, height growth was negatively related to VSWC and positively related to the degree of soil saturation (Table 7). Stem diameter growth of *F. velutina* emergent seedlings was positively related to VSWC and soil porosity (Table 7).
Planted seedling survival and growth

Of the 47 seedlings planted for each species, 10 *P. glandulosa*, three *P. pubescens*, and 40 *F. velutina* seedlings leafed out. Of these, only seven *P. glandulosa*, one *P. pubescens*, and 30 *F. velutina* seedlings survived to the end of the experiment. Due to the low sample size, we did not further analyze *P. pubescens* seedling survival or growth. According to the averaged AFT regression models, survival times of both *P. glandulosa* and *F. velutina* seedlings were significantly related to soil variables, but not VSWC, EC, or their interaction (Table 8). However, seedlings of either species that were located at very low VSWC and EC did not survive (Fig. 9). Increases in bulk density significantly prolonged (approximately doubled) survival of *P. glandulosa* and *F. velutina* seedlings (Table 8). For *F. velutina* seedlings, increases in soil porosity and pH also significantly prolonged survival (Table 8).

Planted *F. velutina* seedlings experienced significant growth in height and stem diameter over the course of the growing season, while *P. glandulosa* seedlings only showed significant stem diameter growth (Fig. 16). Height growth of *P. glandulosa* seedlings was limited due to substantial and repeated browsing during the first growing season. Like seedling survival, height and stem diameter growth of *P. glandulosa* and *F. velutina* seedlings in the field were also not significantly related to VSWC or EC (Table 9). Diameter growth of *F. velutina* was significantly and positively related to soil bulk density and air-filled porosity (Table 9). All other parameters were not included or had confidence intervals overlapping zero in the averaged linear mixed models (Table 9).
DISCUSSION

Our results indicate that under controlled conditions, water stress had more negative effects on desert tree regeneration than salinity. Greater inhibition of germination associated with PEG compared to NaCl indicates osmotic water potential is likely the primary stress inhibiting germination, not specific ion effects (Fig. 1). Similarly, water availability had greater negative effects on seedling growth than high salinity under controlled conditions in the greenhouse experiment (Fig. 5).

However, germination and seedling survival occurred across a broad range of water and salinity stresses for all species, indicating that the three dominant tree species at Ash Meadows are highly adapted to these stresses. Water availability and salinity were consistently important to regeneration under controlled conditions and had varying levels of importance for different ontogenetic stages under field conditions. Other soil variables were not consistently important to regeneration, with significant effects primarily on emergent seedlings (Tables 6 and 7), but were correlated with VSWC (Table 1 in Appendix A).

Fundamental niche shifts between ontogenetic stages

Species’ water and salinity tolerances differed substantially between ontogenetic stages under field conditions. The ontogenetic shifts of seed and seedling responses to water and salinity stresses were consistent across species. All species had seedlings emerge from planted seeds and survive to the end of the experiment in areas with no naturally occurring background emergence, indicating seed dispersal is limited relative to the availability of suitable habitat for seedlings (Turnbull et al. 2000). Most importantly,
the soil water and salinity conditions under which emergent seedlings survived were substantially narrower than those under which seedlings emerged and older planted seedlings and mature trees survived in the field (Fig. 9). The niche contraction observed to occur between seed and emergent seedling stages indicates that germination cuing by water and salinity conditions may not be an effective mechanism of habitat selection for any of these species (Donohue et al. 2010). Germinability under salt or drought stress is not well correlated with salinity or drought tolerance at later developmental stages (Almansouri et al. 2001; Murillo-Amador et al. 2002). Additionally, seed germination is unlikely to respond to variation in soil fertility or other environmental factors only relevant to seedlings survival that could have varied between plots. This discordance between where seeds are dispersed and seedlings can establish may lead to spatial and temporal variation in which locations are most suitable for recruitment into the population, restricting abundance patterns (Schupp 1995).

Our results are in line with other studies showing larger seedlings and mature trees surviving under broader conditions than smaller seedlings (Parrish and Bazzaz 1985; Donovan et al. 1993). Emergent seedlings of *P. glandulosa* and *F. velutina* were several times smaller than planted seedlings (Fig. 16) and had much lower survival rates, with survival occurring over a more limited set of soil water and salinity conditions (Fig. 9). Larger seedlings may have been better able to survive abiotic stress due to greater rooting depth and thus access to deeper soil water and groundwater (Donovan et al. 1993), which is substantially less saline (George Breit, pers. comm.). Soil water availability was highest in the spring, when the root system of emergent seedlings is limited in extent, and decreased as summer progressed (Fig. 8). Also, greater drought
tolerance of older, larger seedlings to water stress may represent a physiological response
to shifting water availability patterns over the growing season (e.g., Amlin and Rood
2002).

**Fundamental niche differences between species**

The optimal water and salinity levels for germination and seedling emergence
differed between species, with lower water and higher salinity for *P. glandulosa*, lower
water and lower salinity for *P. pubescens*, and higher water and lower salinity for *F.
velutina* (Figs. 1 and 11–13). Germination of *Prosopis* species exhibited a higher degree
of salt tolerance than expected given previously reported germination experiments on
seeds from other areas, suggesting there may be local adaptation to the high salinity
conditions found at Ash Meadows. Jackson et al. (1990) reported no germination of *P.
glandulosa* at NaCl concentrations of 242 mol m⁻³ or above in a similar laboratory study,
while we found a germination proportion of 0.98±0.01 at 397 mol m⁻³ (Ψₛ = -2 MPa) and
0.90±0.04 at 595 mol m⁻³ (Ψₛ = -3 MPa). For *P. pubescens*, Jackson et al. (1990) reported
no germination at NaCl concentrations at or above 121 mol m⁻³, while we found a
0.99±0.01 germination proportion at 116 mol m⁻³ (Ψₛ = -1 MPa) and suboptimal
germination of 0.12±0.08 at our maximum salinity of 595 mol m⁻³ (Ψₛ = -3 MPa). In
contrast to the single pulse of germination observed by Jackson et al. (1990), we also
found that germination occurred over several weeks for both *Prosopis* species, with
germination delayed at lower water potentials (Fig. 2). Germination rates for *F. velutina*
were significantly lower than those for both *Prosopis* species across all water potentials,
with no germination occurring below Ψₛ = -1.0 MPa. The salinity range under which
germination occurs and pattern of decreasing germination rates at lower osmotic potentials (i.e., higher salinities) is consistent with the results of Liu (2010) using *F. velutina* seeds from its introduced range in China.

In the field, emergent seedlings of both *Prosopis* species survived at intermediate VSWC, while emergent *F. velutina* seedlings that survived were at higher VSWC (Fig. 9). Larger seedlings of all species survived across a wide range of water availability and salinity levels under controlled conditions (Fig. 3) or in the field (Fig. 9). Survival rates and growth responses of both *Prosopis* species at high salinities were similar to other reports (Jackson et al. 1990). In the greenhouse experiment, there was a significant interaction between water availability and salinity, with maximum growth occurring at lower salinities under shallow water tables, but local maxima shifting to intermediate salinities at intermediate water levels, particularly for *P. glandulosa* and *P. pubescens* seedlings (Table 3; Fig. 5). This growth response is characteristic of halophytic species (Flowers et al. 1986). The differences in responses of species to water and salinity stress correspond to differences in tree morphology and physiology. *Prosopis* species are highly adapted to water stress, primarily through deep tap roots, while *F. velutina* has a ball root structure that limits its rooting depth to ~5 m (Stromberg et al. 1996; Midwood et al. 1998; Snyder and Williams 2000). Leaf physiology suggests that *F. velutina* is adapted to more mesic conditions, but can substantially limit transpiration under experimental drought conditions (average VSWC of 0.094±0.076) while maintaining growth (Balok and St. Hilaire 2002).
Potential mechanisms of stress tolerance

The convergence between species in the patterns of age-specific responses suggests these species share similar physiological stress tolerance mechanisms. Seed dormancy provides a bet-hedging strategy where there is temporal variability in the suitability of conditions for germination and seedling establishment (Baskin and Baskin 1998; Donohue et al. 2010). Seeds that germinated later in the growing season maintained viability through exposure to the full range of VSWC and EC conditions at the plot. Seeds of both Prosopis species germinated within a period of a few weeks in the laboratory experiment (Fig. 2), but seedling emergence occurred over a few months in the field experiment (Figs. 11–13). The generally slower germination rate of pre-treated F. velutina is likely related to its morphophysiological dormancy as opposed to the physiological dormancy of Prosopis seeds (Baskin and Baskin 2005). Seeds of all species exhibited osmotic recovery, indicating mechanisms to cue germination when conditions are favorable for germination (Donohue et al. 2010). This adaptation allows seeds to germinate during the infrequent periods when salinity is low due to high rainfall, which causes salts to leach deeper into the soil, or the water table is high, which dilutes the concentration of salts at the soil surface (Pujol et al. 2000).

Because germination and growth occurred under a range of conditions, it is likely that seeds and seedlings were able to accumulate solutes within cells to decrease water potential across the cell membrane and absorb more water (i.e., osmotic adjustment). The interactive effects of salinity and water availability on growth (Figs. 1 and 15) may be indicative of this mechanism. Osmotic adjustment through accumulation of Na\(^+\) and Cl\(^-\) ions has been found to be important in P. glandulosa and related species (Jarrell and
Under saline conditions, *F. velutina* leaves have been found to accumulate Na\(^+\) at the expense of K\(^+\), potentially leading to ion imbalance and toxicity, but also accumulate the amino acid proline (Wu et al. 2000). Proline plays a pivotal role in osmotic adjustment, defends against reactive oxygen species, and signals other mechanisms of stress tolerance (Hayat et al. 2012). It is likely that *P. glandulosa* and *P. pubescens* also accumulate compatible solutes as do other *Prosopis* species (Meloni et al. 2004; Llanes et al. 2013). Seedlings also exhibited phenotypic plasticity in response to low water availability, significantly increasing the root: shoot ratio at the lowest depth to water (Fig. 6). An increased allocation to roots may aid in obtaining water and nutrients (Chaves et al. 2002). We did not observe this response to salinity stress, although it has been observed at salinities of 600 mol m\(^-3\) in *P. alba* (Meloni et al. 2004).

**Comparison between experimental methods**

Using both controlled laboratory and greenhouse experiments and field experiments allowed us to better parse the interactive effects of water and salinity on the ontogenetic stages of regeneration. The general pattern of plant responses to water and salinity stress under controlled and field conditions was very similar. Germination, seedling emergence, and seedling survival occurred under a broad range of water and salinity stresses, particularly for the *Prosopis* species. Although results of the field experiment for *P. pubescens* were limited due to scarce leaf out and low sample sizes, the general agreement between experiments increases confidence in the results. The only sizeable mismatch between the experiments occurred in survival patterns for young
seedlings; survival was much higher and occurred across a greater range of water and salinity levels for seedlings in the greenhouse experiment than for emergent seedlings in the field experiment (Figs. 3 and 9). This likely occurred because environmental factors that may also influence seedling establishment (e.g., herbivory, light, temperature, soil fertility) were not measured in the field and were controlled in the greenhouse experiment. We observed herbivory of *Prosopis* seedlings that significantly affected plant growth, but did not lead to mortality over the course of the field experiment. We attempted to control for plant-plant interactions and canopy effects on light levels in the field experiment by removing the aboveground portion of all competing vegetation and placing these plots in tree canopy interspaces. Variation in surface soil temperature was significantly related to VSWC (data not shown). We did not measure soil nutrients, but soils with high Na⁺ reduce the availability of other cations to plants and soils with high pH are associated with reduced availability of trace minerals and phosphates (Qadir and Schubert 2002).

Our experimental approach also allowed us to explicitly eliminate the effects of seed dispersal on seedling regeneration. This approach is particularly useful in species where regeneration is a rare event, and thus difficult to observe. Observational approaches cannot readily identify species’ underlying stress tolerances and are better suited to identifying the realized niche as influenced by a variety of potentially confounding ecological processes.
CONCLUSIONS

Regeneration, and particularly survival of young seedlings, is strongly limited by water and salinity stress for the three desert tree species we examined. The fundamental niche and spatial pattern of regeneration differ predictably across ontogenetic stages and species. The ontogenetic niche shifts may represent changes in species’ tolerances to environmental conditions, particularly water and salinity stresses. This suggests that it is necessary to conceptualize and model ecological niches across ontogenetic stages to predict the effects of novel environments (e.g., climate change, species invasions) on species distributions and plant communities.

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REFERENCES


**Tables**

**Table 1.** Results of two-way ANOVA for germination proportion of pre-treated seeds of three desert tree species under six levels of water potentials ($\Psi_s$) and two different osmotic agents (OA).

<table>
<thead>
<tr>
<th>Species</th>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. glandulosa</em></td>
<td>$\Psi_s$</td>
<td>5</td>
<td>0.27</td>
<td>24.84</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>OA</td>
<td>1</td>
<td>0.96</td>
<td>88.39</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>$\Psi_s \times OA$</td>
<td>4</td>
<td>0.21</td>
<td>18.88</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>33</td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. pubescens</em></td>
<td>$\Psi_s$</td>
<td>5</td>
<td>1.20</td>
<td>401.25</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>OA</td>
<td>1</td>
<td>0.35</td>
<td>115.55</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>$\Psi_s \times OA$</td>
<td>4</td>
<td>0.25</td>
<td>82.39</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>33</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>F. velutina</em></td>
<td>$\Psi_s$</td>
<td>5</td>
<td>0.07</td>
<td>36.18</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>OA</td>
<td>1</td>
<td>0.03</td>
<td>16.20</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>$\Psi_s \times OA$</td>
<td>4</td>
<td>0.02</td>
<td>10.93</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>77</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Mean germination proportion and time to germination (±SE) for seeds of three desert tree species exposed to six levels of water potentials ($\Psi_s$) under two osmotic agents. Letters represent significant differences within columns according to Tukey’s test.

<table>
<thead>
<tr>
<th>$\Psi_s$</th>
<th>Osmotic agent</th>
<th>Germination proportion</th>
<th>Time to germination</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>P. glandulosa</td>
<td>P. pubescens</td>
</tr>
<tr>
<td>0</td>
<td></td>
<td>1±0$^a$</td>
<td>1±0$^a$</td>
</tr>
<tr>
<td>-0.5</td>
<td>NaCl</td>
<td>1±0$^a$</td>
<td>1±0$^a$</td>
</tr>
<tr>
<td>-1</td>
<td>NaCl</td>
<td>0.99±0.01$^a$</td>
<td>0.99±0.01$^a$</td>
</tr>
<tr>
<td>-1.5</td>
<td>NaCl</td>
<td>0.97±0.01$^{ab}$</td>
<td>0.98±0.01$^{ab}$</td>
</tr>
<tr>
<td>-2</td>
<td>NaCl</td>
<td>0.98±0.01$^a$</td>
<td>0.85±0.03$^b$</td>
</tr>
<tr>
<td>-3</td>
<td>NaCl</td>
<td>0.90±0.04$^{ab}$</td>
<td>0.12±0.08$^c$</td>
</tr>
<tr>
<td>-0.5</td>
<td>PEG</td>
<td>0.97±0.03$^{ab}$</td>
<td>0.99±0.01$^a$</td>
</tr>
<tr>
<td>-1</td>
<td>PEG</td>
<td>0.98±0.02$^a$</td>
<td>0.99±0.01$^a$</td>
</tr>
<tr>
<td>-1.5</td>
<td>PEG</td>
<td>0.72±0.08$^{bc}$</td>
<td>0.97±0.01$^{ab}$</td>
</tr>
<tr>
<td>-2</td>
<td>PEG</td>
<td>0.48±0.10$^c$</td>
<td>0.04±0.03$^c$</td>
</tr>
<tr>
<td>-3</td>
<td>PEG</td>
<td>0.14±0.10$^d$</td>
<td>0.02±0.02$^c$</td>
</tr>
</tbody>
</table>
Table 3. Significance of the effects of the interaction between depth to water and salinity treatments on the intercept and slope of linear mixed models of height and leaf number for each tree species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Height Intercept $\chi^2$</th>
<th>Height Slope $\chi^2$</th>
<th>Leaf number Intercept $\chi^2$</th>
<th>Leaf number Slope $\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P. $ glandulosa</td>
<td>41.73 0.013</td>
<td>235.54 &lt;0.001</td>
<td>24.25 0.448</td>
<td>131.70 &lt;0.001</td>
</tr>
<tr>
<td>$P. $ pubescens</td>
<td>46.52 0.003</td>
<td>142.03 &lt;0.001</td>
<td>103.94 &lt;0.001</td>
<td>409.13 &lt;0.001</td>
</tr>
<tr>
<td>$F. $ velutina</td>
<td>71.09 &lt;0.001</td>
<td>160.20 &lt;0.001</td>
<td>71.91 &lt;0.001</td>
<td>219.52 &lt;0.001</td>
</tr>
</tbody>
</table>

Table 4. Summary statistics for measurements of soil variables measured in the field experiment.

<table>
<thead>
<tr>
<th>Soil variable</th>
<th>Mean</th>
<th>SD</th>
<th>Min</th>
<th>Median</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Volumetric soil water content</td>
<td>0.18</td>
<td>0.14</td>
<td>0.002</td>
<td>0.16</td>
<td>0.81</td>
</tr>
<tr>
<td>Electrical conductivity (dS m$^{-1}$)</td>
<td>20.40</td>
<td>17.98</td>
<td>0.40</td>
<td>13.78</td>
<td>75.40</td>
</tr>
<tr>
<td>Bulk density (g cm$^{-3}$)</td>
<td>1.23</td>
<td>0.49</td>
<td>0.22</td>
<td>1.11</td>
<td>3.30</td>
</tr>
<tr>
<td>pH</td>
<td>8.92</td>
<td>0.64</td>
<td>7.58</td>
<td>8.91</td>
<td>10.47</td>
</tr>
<tr>
<td>Porosity</td>
<td>0.30</td>
<td>0.08</td>
<td>0.14</td>
<td>0.30</td>
<td>0.63</td>
</tr>
<tr>
<td>Air-filled porosity</td>
<td>0.16</td>
<td>0.09</td>
<td>0.01</td>
<td>0.15</td>
<td>0.51</td>
</tr>
<tr>
<td>Degree of saturation</td>
<td>0.47</td>
<td>0.31</td>
<td>0.01</td>
<td>0.46</td>
<td>1.37</td>
</tr>
<tr>
<td>GSWC</td>
<td>0.16</td>
<td>0.13</td>
<td>0.002</td>
<td>0.14</td>
<td>0.72</td>
</tr>
</tbody>
</table>
Table 5. Number of Accelerated Failure Time (AFT) regression models included in model averaging (NM) and model averaged estimated time ratios and 95% confidence intervals (CI) for the timing of seedling emergence of *Prosopis glandulosa* (*n* = 2 models), *P. pubescens* (*n* = 2 models), and *Fraxinus velutina* (*n* = 1 model) in the field. Confidence intervals that do not overlap one indicate significance.

<table>
<thead>
<tr>
<th>Model parameter</th>
<th>P. glandulosa</th>
<th>P. pubescens</th>
<th>F. velutina</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NM</td>
<td>Time ratio</td>
<td>Lower CI</td>
</tr>
<tr>
<td>(Intercept)</td>
<td></td>
<td>288.56</td>
<td>142.48</td>
</tr>
<tr>
<td>VSWC</td>
<td>2</td>
<td>0.90</td>
<td>0.63</td>
</tr>
<tr>
<td>EC</td>
<td>2</td>
<td>1.01</td>
<td>1.00</td>
</tr>
<tr>
<td>VSWC x EC</td>
<td>2</td>
<td>0.98</td>
<td>0.97</td>
</tr>
<tr>
<td>Bulk density</td>
<td>2</td>
<td>2.60</td>
<td>2.41</td>
</tr>
<tr>
<td>pH</td>
<td>2</td>
<td>0.89</td>
<td>0.83</td>
</tr>
<tr>
<td>Porosity</td>
<td>2</td>
<td>0.15</td>
<td>0.06</td>
</tr>
<tr>
<td>Air-filled porosity</td>
<td>1</td>
<td>1.54</td>
<td>0.85</td>
</tr>
<tr>
<td>Degree of saturation</td>
<td>2</td>
<td>0.48</td>
<td>0.36</td>
</tr>
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</table>
Table 6. Model averaged parameter relative importance (RI), estimated time ratios, and 95% confidence intervals (CI) for time ratios for Accelerated Failure Time (AFT) regression models of the timing of survival of seedlings planted in the field for *Prosopis glandulosa* (n = 5 models), *P. pubescens* (n = 2 models), and *Fraxinus velutina* (n = 11 models). Confidence intervals that do not overlap one indicate significance.

<table>
<thead>
<tr>
<th>Species</th>
<th>RI</th>
<th>(Intercept)</th>
<th>VSWC</th>
<th>EC</th>
<th>VSWC x EC</th>
<th>Bulk density</th>
<th>pH</th>
<th>Porosity</th>
<th>Air-filled porosity</th>
<th>Degree of saturation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. glandulosa</em></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.19</td>
<td>1</td>
<td>0.08</td>
<td>0.08</td>
<td>0.14</td>
</tr>
<tr>
<td>Time ratio</td>
<td>0.04</td>
<td>1579.83</td>
<td>1.08</td>
<td>0.63</td>
<td>0.96</td>
<td>2.04</td>
<td>1.6</td>
<td>1.17</td>
<td>1.17</td>
<td>0.97</td>
</tr>
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Table 7. Model averaged relative importance (RI), estimate (Est), SE, and 95% confidence intervals (CI) for linear mixed models of height and diameter growth of seedlings that emerged from seeds planted in the field of *Prosopis glandulosa* (n = 6 and 3 models, respectively), *P. pubescens* (n = 1 and 2 models, respectively), and *Fraxinus velutina* (n = 2 and 1 models, respectively). Confidence intervals that do not overlap one indicate significance.

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Table 8. Model averaged parameter relative importance (RI), estimated time ratios, and 95% confidence intervals (CI) for time ratios for Accelerated Failure Time (AFT) regression models of the timing of survival of planted seedlings of *Prosopis glandulosa* (n = 31 models) and *Fraxinus velutina* (n = 21 models) seedlings. Confidence intervals that do not overlap one indicate significance.

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<th>pH</th>
<th>Porosity</th>
<th>Air-filled porosity</th>
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Table 9. Model averaged relative importance (RI), estimate (Est), SE, and 95% confidence intervals (CI) for linear mixed models of planted seedling height and diameter growth for *Prosopis glandulosa* (n = 14 and 8 models, respectively) and *Fraxinus velutina* (n = 3 and 2 models, respectively) in the field experiment. Confidence intervals that do not overlap one indicate significance.

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FIGURES

Figure 1. Germination proportion (±SE) of seeds of three desert tree species across a range of water potentials under two osmotic agents (NaCl and PEG, m.w. 8000) and after recovery in deionized water.
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CHAPTER 3. PLANT-PLANT INTERACTIONS INFLUENCE TREE
ESTABLISHMENT IN DESERT WETLANDS: A FIELD TEST OF THE STRESS
GRADIENT HYPOTHESIS

ABSTRACT

Plant interactions are ubiquitous in terrestrial ecosystems and the net effect of these
interactions has been found to vary along stress gradients. Specifically, the stress gradient
hypothesis predicts that net facilitation should be stronger or more frequent at higher
abiotic stress. We conducted a field experiment to examine how the effects of understory
and overstory vegetation on seedling establishment of *Prosopis glandulosa*, *P.
pubescens*, and *Fraxinus velutina* changed along resource (water) and abiotic stress
(salinity) gradients and to examine how vegetation ameliorated stressful conditions along
those gradients. Vegetation significantly ameliorated both water and salinity stresses. We
found that interactions between vegetation treatments and stress gradients were variable
between species and life stages and changed in association with plant cover. There was a
clear increase in facilitation of *P. glandulosa* seedling emergence and emergent seedling
survival along a water availability gradient in concordance with the stress gradient
hypothesis. For *F. velutina*, there was a significant interaction between vegetation
treatment and the salinity gradient that led to variable relationships associated with
vegetation type and the amount of plant cover. Results suggest a general, predictable
pattern of shifts in the net outcome of plant-plant interactions for establishment of tree
species in groundwater-driven desert environments, from net facilitation (seedling
emergence stage) to net competition (survival of newly emergent seedlings) and
ultimately to net neutrality (established seedlings rooted in the water table).
INTRODUCTION

Both competitive and facilitative plant interactions have been found to be of great importance in arid environments, but the net effects of these interactions along stress gradients can be quite variable (Gomez-Aparicio et al. 2004; Maestre et al. 2005; Lortie and Callaway 2006). The stress gradient hypothesis predicts that the net outcome of plant interactions varies predictably along stress gradients, with net facilitation more common on more stressful sites and net competition more common on less stressful sites (Bertness and Callaway 1994; Callaway and Walker 1997). Studies examining these relationships have often observed functional relationships that are unimodal, with facilitation occurring at intermediate stress, rather than the original monotonic relationship initially proposed, particularly for water stress gradients in arid environments (Maestre et al. 2005, 2009; Lortie and Callaway 2006; Brooker et al. 2008). A number of factors have been proposed to influence the outcome of studies examining these relationships, including resource versus non-resource stress gradients, interactions among multiple stress factors (Kawai and Tokeshi 2007), species stress tolerances (Gross et al. 2010), and ontogenetic shifts (Tielborger and Kadmon 2000; Miriti 2006; Sthultz et al. 2007; le Roux et al. 2013). The use of observational methods versus experimental plantings or competitor removal may also lead to different interpretations of the importance of facilitation because plants generally experience positive and negative interactions (Michalet 2006; Gross et al. 2010).

In arid ecosystems, water availability and salinity are the most likely factors to limit species distributions (Chapter 2 and Noy-Meir 1973; Ungar 1991) and competition is intense, even where there are facilitative interactions (Maestre et al. 2003). Water
provides a necessary resource and also is a source of physiological stress, so the importance of facilitation is predicted to have a unimodal relationship because at high stress either competitive effects or the extreme stress itself may outweigh any facilitative effects of other vegetation (Tielborger and Kadmon 2000; Maestre and Cortina 2004; Michalet 2006; Maestre et al. 2009). In contrast, salinity is solely a stress and the importance of facilitation is predicted to increase linearly with stress (Maestre et al. 2009). In arid environments, seedling establishment is a crucial ontogenetic stage that is particularly vulnerable (Schupp 1995; Weiher and Keddy 1995; Kitajima and Fenner 2000) because seeds and seedlings are exposed to the drier, more saline conditions near the soil surface. Facilitation from understory vegetation is expected to be important for physiologically stressed seedlings that can escape or tolerate stress more effectively during later life stages (Parrish and Bazzaz 1985; Tielborger and Kadmon 2000; Miriti 2006; Bonanomi et al. 2011). However, the outcome of plant interactions can be highly variable in arid environments, particularly under high stress conditions in which competitive effects dominate or where facilitative amelioration of stress is insufficient (Tielborger and Kadmon 2000; Maestre and Cortina 2004; Michalet et al. 2006; Maestre et al. 2009). As seedlings of woody species mature and grow in size, there is generally a shift from facilitative to neutral or competitive interactions (Miriti 2006; Sthultz et al. 2007; le Roux et al. 2013).

In this paper, we investigate the response of seedling establishment (including both seedling emergence and survival) of three desert tree species to understory and overstory plant interactions along water and salinity stress gradients. We chose to examine seedling establishment because regeneration is a crucial bottleneck for plant
population dynamics and a dominant influence on plant population structure (Grubb 1977; Parrish and Bazzaz 1985). We addressed the following questions: (1) How do desert tree seedlings respond to plant interactions across interacting water and salinity gradients? And, (2) how do overstory and understory vegetation affect soil water content and salinity? To this end, we conducted a field experiment in which we measured the stress gradients, changes in abiotic stress associated with plants, and seedling establishment in relation to both plant interactions and the abiotic stress gradients.

**METHODS**

**Study area**

Ash Meadows National Wildlife Refuge is a 9310-ha wetland complex in Amargosa Valley, NV (36°25’12”N, 116°19’48”W; ca. 670 m a.s.l.). The climate is typical of the northern Mojave Desert, with average high temperatures of 40°C in summer, average low temperatures of -1°C in winter, and average annual precipitation of 10 cm. Soils are generally immature and poorly developed, with dominant soil orders including Aridisols in upland areas and younger Entisols and Inceptisols where there are alluvial deposits. The refuge contains over 30 springs and seeps that discharge 16,500 to 17,500 ac-ft yr⁻¹ (Otis Bay Inc and Stevens Ecological Consulting 2006), leading to strong spatial gradients in water availability related to depth to groundwater and distance to surface water. Salts accumulate on the soil surface in areas with shallow groundwater. Common salt forms include halite (NaCl), thenardite (Na₂SO₄), and trona (Na₃H(CO₃)₂·2H₂O) (George Breit, pers. comm.).
Dominant vegetation varies with water availability: emergent wetlands (*Typha* spp., *Scirpus* spp., and *Eleocharis* spp.) occur where surface water is present, savannas (*Carex* spp., *Juncus* spp., *Distichlis spicata*, and *Sporobolus airoides* grasses and trees) and sparsely vegetated dunes occur where groundwater is relatively shallow, and alkali and desert scrub occur in drier upland areas (*Atriplex* spp., *Lycium* spp., and *Larrea tridentata* [DC.] Cov.). Trees primarily occur in the savanna and dune systems where groundwater is accessible. The three dominant tree species are *Prosopis glandulosa* var. *torreyana* [L. Benson] M. Johnson (western honey mesquite), *P. pubescens* Benth. (screwbean mesquite), and *Fraxinus velutina* Torr. (velvet ash).

**Seed and seedling materials**

Seeds were collected from across Ash Meadows from September – November 2008 from 17 sites for use in growing seedlings and from September – November 2009 from 12 sites for direct sowing into the field experiment. We collected mature *F. velutina* seeds directly from the tree and collected *Prosopis* legumes from both the tree and ground from at least ten trees per site. Seeds were pre-treated before planting. We cold stratified *F. velutina* seeds at 7°C and stored all *Prosopis* seeds at room temperature for 55-70 days prior to planting. Within 48 hours before planting, we mechanically scarified *P. glandulosa* seeds by nicking (Vilela and Ravetta 2001) and chemically scarified *P. pubescens* seeds using a 98% H$_2$SO$_4$ bath for 30 minutes (Jackson et al. 1990), and then soaked them in cold water for 12 hours.

All *Prosopis* seedlings and 62% of *F. velutina* seedlings were grown from seeds collected across Ash Meadows in September – November 2008. These seedlings were
grown in 0.41-m deep pots (TPOT2, Stuewe & Sons, Tangent, OR) in the greenhouses at University of Nevada – Reno from March to August 2009 and then hardened outdoors until planting. The remaining *F. velutina* seedlings were grown from field collected seeds at College of Southern Nevada (Henderson, NV), in 17.2-cm deep garden pots from March 2007 to January 2009.

**Field experiment**

We identified two sites with strong gradients in soil water content and salinity and located two transects parallel to the gradient within each site. We used changes in plant species composition along the gradient to define zones with similar environmental conditions. We subjectively located two representative plots within 10 m of the transect that were not under tree canopies (n = 47) and zero to two plots under trees of each species within 25 m of the transect. Because trees were not randomly distributed along the gradient, not all tree species are represented in each zone and species are represented unequally (n = 6 for *P. glandulosa*, n = 17 for *P. pubescens*, and n = 21 for *F. velutina*).

Treatments included no vegetation (cleared understory vegetation/no canopy cover), understory vegetation (intact understory vegetation/no canopy cover), and overstory vegetation (cleared understory vegetation/canopy cover). All plots without canopy cover contained six 2 x 1-m subplots; we randomly selected half of the subplots for hand-removal of all understory vegetation and litter and randomly assigned one no vegetation and one understory vegetation subplot to each species. Because we removed vegetation, the no vegetation treatment was not a control. For overstory treatment plots beneath tree canopies, we removed all vegetation and litter within 1 m of the bole for
trees with canopy areas less than 6 m² and cleared vegetation and litter in 2 x 1 m plots for trees with larger canopy areas to better isolate the effects of overstory vegetation. We found no effect of tree size or plot characteristics on germination or seedling survival, and thus excluded them from further analysis. We standardized the location of subplots around trees at azimuths of 0°, 120°, and 240° and randomized placement of each species.

We divided the subplots into two equal partitions and planted a single dormant seedling in the center of one half of each subplot in January - February 2010. In plots with intact understory vegetation, we removed as little vegetation and litter as possible and replaced surface litter after planting. Of the 138 planted seedlings of each species, leaf out occurred for 28 *P. glandulosa* seedlings (nine, 11, and 8 seedlings in the no vegetation, understory vegetation, and overstory vegetation treatments, respectively), 10 *P. pubescens* seedlings (three, six, and one seedling in the no vegetation, understory vegetation, and overstory vegetation treatments, respectively) and 117 *F. velutina* seedlings (39, 42, and 36 seedlings in the no vegetation, understory vegetation, and overstory vegetation treatments, respectively).

We also planted 10 (*P. glandulosa* and *P. pubescens*) or 50 (*F. velutina*) pre-treated seeds, reflecting their probability of germination under optimal conditions (Chapter 2), in the half of each treatment subplot not containing a planted seedling (n = 47 plots x 10 or 50 seeds for the no vegetation and understory vegetation treatments and n = 44 plots x 10 or 50 seeds for the overstory vegetation treatment). Seeds were shallowly buried at 0.5-cm depth to improve the probability of the radicle penetrating the soil. We provided no supplemental water to seeds or seedlings.
We monitored seedling emergence, growth, and survival every 1 – 3 months during the growing season (March to November). Seedling emergence was monitored during the 2010 growing season, while seedling growth and survival were monitored in the 2010 and 2011 growing seasons and in May 2012. During each monitoring event, we marked seedling emergence with toothpicks color-coded for date of emergence. We also recorded seedling height, stem diameter at the root crown, and number of photosynthetically active leaves as measures of seedling size. Seedlings that emerged from planted seeds reached a maximum age of two years by the end of the experiment, while those that were planted as seedlings in the field were able to reach three to five years.

At each monitoring date, we visually estimated plant cover and measured soil water availability and salinity to quantify the water stress gradient along each transect. We collected surface soil samples from 0 to 10-cm depth in representative subplots in the no vegetation and understory vegetation subplots that were not under canopy cover and from the 0° azimuth subplot with overstory vegetation. After taking relevant measurements, we removed aboveground understory vegetation and litter to maintain the no vegetation and overstory vegetation treatments. Soil samples were weighed, dried at 105°C for 72 hours, and reweighed to calculate gravimetric soil water content (GSWC) and bulk density (BD). Soil samples were wetted to saturation using deionized water to determine total porosity and for measurement of electrical conductivity (EC) and pH. We calculated volumetric soil water content (VSWC), air-filled porosity, and degree of saturation from these measurements.
Analysis of the abiotic environment

Soil VSWC and EC measurements in the no vegetation subplots were interpreted as proxy variables for defining water and salinity stress gradients to assist in the identification of the effects of vegetation treatments on soil water and salinity. We used these proxies because the net effects of vegetation on VSWC and EC were expected to differ based in part on plot VSWC and EC; for example, vegetation in a very wet plot may reduce VSWC relative to the no vegetation treatment, while vegetation at a plot with intermediate water availability might increase VSWC relative to the no vegetation treatment. To determine the effects of vegetation treatment on soil VSWC and EC, we used linear mixed effects models with a random effect of vegetation treatment nested within plot. Fixed variables included vegetation treatment and sampling month as factors and the water or salinity stress gradient (i.e., VSWC or EC in subplots with no vegetation) as applicable, percent cover of plants in subplots with understory vegetation, and time since the start of the experiment as continuous variables. The models included three-way interactions between vegetation treatment, the applicable stress gradient, and the remaining variables. We included the interaction with plant cover because the effects of understory vegetation on soil VSWC and EC may be minimal in plots with little plant cover. Perennial grass dominated plant cover across the water stress gradient except at plots with VSWC < 0.1, where shrubs were the dominant cover (unpubl. data), so we did not include understory species composition as a model factor. We included the interactions with sampling month and time since the start of the experiment because the difference between treatments along the stress gradients may change seasonally in response to climatic conditions and over time. Mixed effects models were fit using
package ‘lme4’ (ver. 0.999999-2) in the R statistical environment (ver. 3.0.1; R Foundation for Statistical Computing 2013).

Analysis of seedling establishment

We modeled the effects of vegetation treatments and stress gradients on seedling emergence and survival of each tree species. For each analysis, we examined the full set of additive and interaction models for the factor of vegetation treatment and continuous variables of water stress gradient (i.e., VSWC in subplots with no vegetation), salinity stress gradient (i.e., EC in subplots with no vegetation), and plant cover in subplots with understory vegetation, with additional random effects and covariates as specified below.

We used an information theoretic approach to select models and determine model coefficients. In our approach, models were ranked using AICc, a second order form of Akaike’s Information Criterion that corrects for small sample sizes. Models with lower AICc are more likely to be the best model in the candidate set, so we estimated parameter effects using model averaging of predictions based on Akaike weights of models with ΔAICc < 4 compared to the minimum model AICc.

We analyzed the effects of vegetation treatment and stress gradients on seedling establishment using survival analysis, which accounts for censored data (e.g., missing individuals or unobserved deaths) and can predict the effects of cumulative stresses on mortality rates. In this framework, the probability of emergence measures the proportion of individuals that may still emerge at a later date, and thus decreases as more seedlings emerge (Onofri et al. 2010). Emergence data were left censored (mean±SD interval of 39.0±18.0 days) and survival data were interval censored (mean±SD interval of
63.69±74.77 days), with variation reflecting differences in sampling intensity across seasons and years. We constructed emergence and survival functions for each species under each vegetation treatment using parametric estimates of Kaplan-Meier curves and compared them using log-rank tests. Emergence and survival for each species were modeled via parametric Accelerated Failure Time (AFT) regression using the Weibull distribution, in which the mortality rate is proportional to a power function of time. Results of AFT regression can be interpreted using time ratios to describe the expansion or contraction of time to events or as relative risks in the proportional hazards framework (Garson 2012). We reported the estimated model parameters and relative risks in the proportional hazards framework. A decrease in relative risk indicates a decrease in the instantaneous probability of emergence (i.e., a decrease in emergence) or death (i.e., an increase in survival).

For AFT regression models, we used a frailty modeling approach (akin to a mixed model; Pan 2001), in which plots defined clusters (akin to a random effect). For each species, we modeled seedling emergence, survival of planted seedlings (P. glandulosa and F. velutina only due to a sampling size of only 10 for P. pubescens), and survival of emergent seedlings. Candidate models ranged from a null model including only the frailty term (i.e., random effect of plots) to the most complex model, which included a four-way interaction between vegetation treatment, the water and salinity stress gradients, and plant cover. We included covariates for seedling emergence timing and year of seedling emergence in models of survival of emergent seedlings. AFT regression models were fit using package ‘survival’ (ver. 2.37-4) in the R statistical environment.
RESULTS

Abiotic environment

Frequency distributions of the water and salinity stress gradients were both highly right-skewed, with the majority of plots located in areas with low VSWC and EC (Fig. 1). Soil VSWC was significantly affected by interactions between vegetation treatment, the water stress gradient, and the covariates plant cover, sampling month, and time since the start of the experiment (Table 1; Figs. 2 and 3). Interactions between vegetation treatment and the water stress gradient resulted in both understory and overstory vegetation being associated with a decrease in VSWC on the wet end and an increase in VSWC on the dry end of the water stress gradient, with the direction of the interaction changing at a VSWC of ~0.25 along the water stress gradient (Fig. 2). Plant cover was positively related to the magnitude of the increase in VSWC at the dry end of the water stress gradient for both vegetation treatments, and only associated with a larger magnitude effect in the overstory vegetation treatment at the wet end of the gradient (Fig. 3a). Larger magnitude effects of the water stress gradient were also associated with a later sampling month in the growing season and later in the experiment for the overstory vegetation treatment (Fig. 3b). The interaction of time was more variable for the understory vegetation treatment. There was a smaller negative effect of understory vegetation on the wet end of the water stress gradient later in the experiment, but a larger positive effect on the dry end of the gradient earlier in the experiment (Fig. 3c).

Soil EC was significantly affected by the interaction between vegetation treatment, the salinity stress gradient, and plant cover and by sampling month (Table 1).
Soil EC in the understory vegetation treatment was linearly related to the underlying salinity stress gradient, while soil EC in the overstory vegetation treatment had a unimodal relationship with the salinity stress gradient (Fig. 2). Vegetation was associated with a decrease in EC on the high salinity end of the gradient and with an increase in EC on the low salinity end (Fig. 2). The magnitude of this effect was inversely related to plant cover for the understory vegetation treatment (Fig. 4). For the overstory vegetation treatment, the magnitude of the effect was inversely related to plant cover on the low salinity end and positively related to plant cover on the high salinity end of the salinity stress gradient (Fig. 4). Electrical conductivity increased significantly over the growing season under all vegetation treatments ($\beta \pm SE = 0.017 \pm 0.07$; Table 1).

**Seedling emergence**

The majority of seeds of all species did not emerge, with average total emergence percentages of 11.75±0.15% for *P. glandulosa* (161 total emergent seedlings), 12.26±0.16% for *P. pubescens* (160 total emergent seedlings), and 5.99±0.10% for *F. velutina* (411 total emergent seedlings; Fig. 5). Maximal seedling emergence occurred on the drier end of the water stress gradient and in the middle of the salinity stress gradient for *P. glandulosa* and on the wetter end of the water stress gradient and less saline end of the salinity stress gradient for *F. velutina* (Fig. 5). Emergence was relatively similar across both stress gradients for *P. pubescens*, except on the wettest and most saline ends (Fig. 5). Seedling emergence of each species was related to vegetation type and the stress gradients (Table 2). Log-rank tests indicate that there were significant differences between the Kaplan-Meier estimates of seedling emergence functions for different
vegetation treatments for *P. glandulosa* ($\chi^2 = 8.2$, df = 2, $P = 0.016$) and *F. velutina* ($\chi^2 = 14.9$, df = 2, $P < 0.001$), but not *P. pubescens* ($\chi^2 = 5.2$, df = 2, $P = 0.076$). There was more seedling emergence in the overstory vegetation treatment for *P. glandulosa* and in the no vegetation treatment for *F. velutina*.

For seedling emergence of *P. glandulosa*, 14 models were selected from the candidate models and their predictions averaged (Table 2). Confidence intervals for the base risk overlapped zero for both vegetation treatments (Table 3), but clear effects of the vegetation treatments were manifested through their interactions with the water and salinity stress gradients and plant cover (Tables 2 and 3; Fig. 6). There was a consistently strong effect of the water stress gradient on seedling emergence, with greater probability of seedling emergence (i.e., higher relative risk) on the wet end of the gradient for seeds planted in the understory vegetation treatment, but on the dry end of the gradient for seeds planted in the no vegetation and overstory vegetation treatments (Fig. 1 in Appendix B). There was a strong interaction with plant cover in the understory vegetation treatment, in which the magnitude of this effect also changed, and a lesser effect of the salinity stress gradient (Fig. 1 in Appendix B). These interactions resulted in a much higher probability of emergence in the understory vegetation treatment compared to the no vegetation treatment at the wet end of the gradient, particularly where plant cover was high (Fig. 6). There was little difference in the probability of emergence associated with the interaction between the understory vegetation treatment and the salinity stress gradient (Table 3). A similar pattern held for the probability of emergence in the overstory vegetation treatment compared to the no vegetation treatment, but with lower magnitude effects (Fig. 7). Here, the interaction between vegetation treatment and the
salinity stress gradient manifested as a larger magnitude probability of emergence at the
more saline end of the gradient (Fig. 7).

For seedling emergence of *P. pubescens*, a single model was selected from all
candidate models as the best fit (Table 2). This model was of similar structure to the
averaged model for *P. glandulosa*, but with several switches in the direction of
relationships. Like *P. glandulosa*, there was a consistently strong and generally positive
effect of the water stress gradient, but with a more substantial interaction with the salinity
stress gradient (Fig. 2 in Appendix B). Contrary to *P. glandulosa*, there was a lower
probability of emergence for the understory vegetation treatment compared to the no
vegetation treatment, with the magnitude of the effect positively associated with the
water stress gradient and plant cover (Fig. 8). Probability of emergence for the overstory
vegetation treatment relative to the no vegetation treatment varied between positive and
negative in association with plant cover (Fig. 8). At low plant cover, the overstory
vegetation treatment had an increased probability of emergence on the dry end of the
water stress gradient and a decreased probability of emergence on the wet end; the
opposite occurred at high plant cover (Fig. 8).

For seedling emergence of *F. velutina*, two models were selected from all
candidate models (Table 2). These models differed in the inclusion of an interaction term,
with the first model (nearly three times as likely as the second) including the interaction
between the water and salinity stress gradients and the second model including the
interaction between the water stress gradient and plant cover (Tables 2 and 3). The no
vegetation treatment had a significantly higher base probability of seedling emergence
than the other treatments, with a 618% increase over the understory vegetation treatment
and a 588% increase over the overstory vegetation treatment (Table 3). These relative risks were manifested in total emergence of 175 seedlings in the no vegetation treatment versus 124 in the understory vegetation treatment and 112 in the overstory vegetation treatment. The water and salinity stress gradients were significant drivers of seedling emergence, with greater probability of emergence at high water availability and salinity (Fig. 3 in Appendix B). As opposed to the Prosopis species, which showed significant interactions between the water stress gradient and vegetation treatments, the most significant interaction for F. velutina occurred between the salinity stress gradient and vegetation treatments (Table 3; Fig. 3 in Appendix B). Probability of emergence was generally higher with vegetation than that in the no vegetation treatment and positively associated with the salinity stress gradient at low plant cover, with the pattern reversing with increasing plant cover (Fig. 9). Probability of emergence given the presence of overstory vegetation was inversely related to the salinity stress gradient, but was consistently lower than for the no vegetation treatment except at high plant cover (Fig. 10).

**Seedling survival**

Survival analysis showed significant effects of vegetation treatment and stress gradients on seedling survival, with the specific effects differing between emergent and planted seedlings and between species (Figs. 11 and 12). Survival rates of emergent seedlings from emergence to the end of the experiment in May 2012 were low (0 to 11.1%) and showed significant differences between vegetation treatments in the Kaplan-Meier estimates of survival functions for P. pubescens and F. velutina, but not for P.
glandulosa, which had only a single surviving seedling (Table 4). Survival of planted seedlings was substantially higher than for emergent seedlings (16.7% to 100%) and there were no significant differences in survival functions between vegetation types (Table 4).

Of the candidate AFT regression models for emergent seedling survival, five models were supported at ΔAIC<4 for *P. glandulosa*, eight models were supported for *P. pubescens*, and a single model was supported for *F. velutina*. There were significant interactions between vegetation treatment and stress gradients in the averaged models of *P. glandulosa* and *F. velutina* emergent seedling survival, but not *P. pubescens* (Tables 5 and 6). There were only significant differences between vegetation treatments in the base relative risk of emergent seedling death for *F. velutina*, with the understory vegetation treatment having a 65.8% (95% CI: 37.1-99.4%) higher base relative risk and the overstory vegetation treatment having an 82.9% (95% CI: 78.7-86.2%) lower base relative risk compared to the no vegetation treatment (Table 6).

The effects of interactions between vegetation treatments and stress gradients on emergent seedling survival were generally driven by the water stress gradient for *P. glandulosa* and the salinity stress gradient for *F. velutina* (Table 6; Figs. 6-9), as was the case for seedling emergence. There were no significant interactions between vegetation treatment and stress gradients for *P. pubescens* (Tables 5 and 6), but the relative risk of seedling death was strongly negatively associated with the water stress gradient and positively associated with the salinity stress gradient to a lesser extent (Fig. 5 in Appendix B). For *P. glandulosa*, relative risk of emergent seedling death was inversely related to the stress gradients (i.e., higher risk of death at lower values), particularly for
the understory and overstory vegetation treatments (Fig. 4 in Appendix B). Taking into account interactions between these gradients and vegetation treatments, relative risk of emergent seedling death was lower in the understory vegetation treatment at low plant cover and higher in that treatment at high plant cover in comparison to the no vegetation treatment (Fig. 6). At low plant cover, the water stress gradient was negatively associated with the relative risk, with the opposite occurring at high plant cover (Fig. 6). This same pattern occurred for the overstory vegetation treatment, with larger magnitude changes in relative risk associated with water stress where plant cover was high (Fig. 7). There were minimal effects of the salinity stress gradient on relative risk between treatments (Table 6).

For *F. velutina*, relative risk of emergent seedling death was negatively associated with the water stress gradient in the no vegetation and understory vegetation treatments, and minimally positively associated with the water stress gradient in the overstory vegetation treatment (Fig. 6 in Appendix B). Relative risk was positively associated with the salinity stress gradient at low plant cover and negatively associated with the salinity stress gradient at high plant cover across all vegetation treatments (Fig. 6 in Appendix B). These interactions manifested as a lower relative risk of death in the understory vegetation treatment compared to the no vegetation treatment at very low plant cover, with the magnitude of the effect positively associated with the salinity stress gradient (Fig. 9). The effect then shifted to a higher relative risk for the understory vegetation treatment where plant cover was higher, with the magnitude of this effect still positively associated with the salinity stress gradient (Fig. 9). There was a smaller effect of the interaction between vegetation treatment and the water stress gradient that led to higher
relative risk of death at low water availability (Table 6; Fig. 9). Relative risks associated with the overstory vegetation treatment were opposite of those associated with the understory vegetation treatment. There was a higher relative risk of death at low plant cover and a lower relative risk of death at high plant cover compared to the no vegetation treatment and the magnitude was positively associated with the salinity stress gradient (Fig. 10). The smaller effect of the water stress gradient was opposite as well, with higher relative risk of death at high water availability (Fig. 10).

For planted seedlings, the relative risk of death was primarily associated with the stress gradients and plant cover, not vegetation treatment (Tables 7 and 8). Of the six models selected for *P. glandulosa*, only three included vegetation treatment, which had weak effects (Table 8) and only interacted with plant cover in one model (Table 7). Of the eight models selected for *F. velutina*, only one included vegetation treatment as an additive effect (Table 7), and the effect was not significant (Table 8). Planted seedling survival was primarily driven by the water stress gradient for both species, with a higher relative risk of death occurring at the dry end (Table 8; Fig. 7 in Appendix B). The salinity stress gradient had a smaller effect and was negatively associated with relative risk of death (Table 8; Fig. 7 in Appendix B).

**DISCUSSION**

This saline desert wetland ecosystem provided an opportunity to explore the nature of interspecific interactions along two stress gradients across wide ranges of salinity and water availability that occurred over short distances, reducing the potential effects of confounding influences. Effects of interactions between vegetation treatments
and stress gradients were variable between species and between ontogenetic stages, with some patterns supporting the stress gradient hypothesis and others opposing it. This variability suggests it is necessary to consider the inherent characteristics of the system and ecophysiological constraints of the species to understand changes in the net effect of plant interactions along stress gradients. We found that seedling establishment of all three tree species was strongly related to both water and salinity stress gradients (Tables 3, 6, and 8; Appendix B), but, when they existed, interactive effects with vegetation were strongly related to one gradient or the other. The direction and magnitude of plant interactions changed significantly along stress gradients for the seedling emergence and young (i.e., emergent) seedling survival stages, but there was no meaningful interaction between vegetation treatment and either stress gradient for older (i.e., planted) seedling survival (Figs. 6-10). This suggests that plant interactions are most important, and hence the stress gradient hypothesis is most relevant, for the seedling emergence stage. Shifts from net facilitation for smaller individuals to net competition with increasing size have been observed in other woody species (Miriti 2006; Stultz et al. 2007; le Roux et al. 2013). Ontogenetic shifts in the importance of biotic interactions along stress gradients are associated with changing resource requirements and stress tolerance; in this case, larger seedlings are likely able to access more abundant and less saline water deeper in the soil profile (Donovan et al. 1993; Snyder and Williams 2007) and may have greater physiological tolerance to stress as seen in other aridland species (Donovan and Ehleringer 1992).

For stress gradients defined by resources (e.g., water), the importance of positive plant interactions is predicted to be unimodally related to abiotic stress because
competitive effects or the extreme stress itself may outweigh the positive effects of environmental amelioration at high stress (Tielborger and Kadmon 2000; Maestre and Cortina 2004; Michalet et al. 2006; Maestre et al. 2009). In opposition to this hypothesis, we found clear support for the linear form of the stress gradient hypothesis in the response of *P. glandulosa* seedling emergence and emergent seedling survival to vegetation along the water stress gradient. High water availability was more stressful than low water availability for seedling emergence (Fig. 5) and there was a strong facilitative effect of understory and overstory vegetation with increasing water availability and plant cover (Figs. 6 and 7). The effects of vegetation on soil VSWC were strongly positive where water availability was low and negative where water availability was high (Table 1; Figs. 2 and 3), improving conditions for *P. glandulosa* across the resource availability gradient. Several studies have found similar effects of plants on water availability (e.g., Raffaele and Veblen 1998) but this effect has not consistently been found in arid ecosystems (Holmgren et al. 1997; Gómez-Aparicio et al. 2008).

The observed switch in facilitative relationships along the water stress gradient can be explained mechanistically by the observed effects of vegetation on water levels. Vegetation clearly ameliorated abiotic stress associated with water (Fig. 2). Herbaceous plants and litter can increase soil water content by decreasing evaporation (Knoop and Walker 1985; Maestre et al. 2003), but may also compete for limited soil water and reduce its availability (Franco and Nobel 1988; Nobel 1989; Sala et al. 1989). Likewise, woody plants can increase water availability by redistributing water from moist soil to drier soil (Caldwell et al. 1998) or reduce water availability through uptake (Forseth et al. 2001). The presence of abundant shallow groundwater at Ash Meadows (Otis Bay Inc
and Stevens Ecological Consulting 2006) suggests that hydraulic redistribution may drive the increase in VSWC at low water availability (Caldwell et al. 1998) in conjunction with shading that reduces evaporation (Knoop and Walker 1985; Maestre et al. 2003).

While survival analysis showed the effects of vegetation treatment differed along the resource gradient (water) for *P. glandulosa*, these effects were more related to the abiotic stress gradient (salinity) for *F. velutina*. High salinity was stressful for seedling emergence and emergent seedlings of *F. velutina*, but not for survival of planted seedlings (Figs. 5 and 12). At low plant cover in the understory vegetation treatment, the pattern of biotic effects conformed to the stress gradient hypothesis, with vegetation having a facilitative effect on seedling emergence and emergent seedling survival that increased along the salinity gradient (Fig. 9). However, this pattern reversed at high plant cover and for the overstory vegetation treatment (Figs. 9 and 10). This relationship may occur because *F. velutina* seeds and seedlings are intolerant of high salinity (Chapter 2) and there were high levels of salinity even in the intact vegetation treatments (Table 1; Figs. 2 and 4) that may not have allowed seedling establishment (Maestre and Cortina 2004; Maestre et al. 2009). Similar results have been reported for salt marsh communities, where alleviation of salinity stress from experimental manipulations can shift plant interactions from facilitative to competitive (Bertness and Shumway 1993).

Interestingly, both herbaceous and woody vegetation had facilitative effects on seedling establishment of these desert tree species. Facilitation of woody species by herbaceous vegetation has rarely been reported while facilitation by woody species (i.e., nurse plants) is relatively common (Bonanomi et al. 2011). Maestre et al. (2003) found
strong competition, but net facilitation of *Pistacia lentiscus* by the grass *Stipa tenacissima*, attributing it to significant microclimatic amelioration.

Our results suggest a general pattern of shifts in the net outcome of plant interactions associated with ontogenetic stage of plant development despite independent responses of different species to the stress gradients. Net facilitation at the seedling emergence stage shifted to net competition at the emergent seedling stage, and then to net neutral interactions for seedling survival of older plants. Net facilitative effects at the seedling emergence stage (Figs. 6 and 9) occurred when there was relatively little belowground competition, possibly because of large resource reserves in seeds and cotyledons (Kitajima and Fenner 2000). The net interaction shifted to competition for emergent seedlings where understory plant cover was high (Figs. 6 and 9), indicating that young seedlings are inferior competitors to herbaceous vegetation. The lack of significant interaction between vegetation treatment and stress gradients for planted seedling survival suggests that larger, more deeply rooted seedlings are able to reach more abundant water lower in the soil profile and escape competition or become better competitors with age.

Our experimental approach avoided some of the problems associated with earlier studies examining plant interactions along stress gradients (reviewed in Brooker et al. 2008). Firstly, we examined both resource and non-resource gradients using a parallel design. Multiple stresses operate simultaneously in natural systems and may exert separate or combined effects on species performance, and the ability of other plant species in the community to ameliorate them may differ. Examination of only one gradient would have resulted in finding a significant interaction between vegetation
treatment and stress gradients for either *P. glandulosa* or *F. velutina*, but not both.

Secondly, we defined stress relative to the species and ontogenetic stage of interest for each abiotic gradient (e.g., Lortie and Callaway 2006). Stress is not applicable to communities as a whole, but to individual species (Körner 2003; Lortie et al. 2004) and, we suggest, even to individual life stages within that species. For some species, there was little difference in seedling survival across a wide range of conditions (Figs. 11 and 12), indicating a limited role of stress, but there was a significant difference in seedling emergence across the same range of conditions (Fig. 5). Thirdly, we examined multiple life stages for an extended period and thus were able to isolate shifts in the effects of plant interactions from shifting environmental conditions (Miriti 2006). These ontogenetic shifts have substantial implications for plant population dynamics and may leave a signature on plant community structure that is difficult to detect without explicitly examining earlier life stages (Grubb 1977; Parrish and Bazzaz 1985).

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REFERENCES


**Tables**

**Table 1.** ANOVA results of the mixed effects analysis of soil volumetric soil water content (VSWC) and electrical conductivity (EC) for the fixed effects of interactions between vegetation treatment, water or salinity stress gradient (stress), and plant cover, sampling month, and time since the start of the experiment. df\textsubscript{NUM} and df\textsubscript{DEN} gives degrees of freedom of the numerator and denominator, respectively.

<table>
<thead>
<tr>
<th>Variable</th>
<th>df\textsubscript{NUM}</th>
<th>df\textsubscript{DEN}</th>
<th>F</th>
<th>P</th>
<th>df\textsubscript{NUM}</th>
<th>df\textsubscript{DEN}</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>VSWC</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
<td>43</td>
<td>3.49</td>
<td>0.039</td>
<td>2</td>
<td>43</td>
<td>1.252</td>
<td>0.296</td>
</tr>
<tr>
<td>Stress</td>
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<td>1352</td>
<td>2397.079</td>
<td>&lt;0.0001</td>
<td>1</td>
<td>1352</td>
<td>388.336</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Plant cover</td>
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<td>45</td>
<td>3.419</td>
<td>0.071</td>
<td>1</td>
<td>45</td>
<td>1.776</td>
<td>0.189</td>
</tr>
<tr>
<td>Month</td>
<td>1</td>
<td>1352</td>
<td>5.194</td>
<td>0.023</td>
<td>1</td>
<td>1352</td>
<td>6.863</td>
<td>0.009</td>
</tr>
<tr>
<td>Time</td>
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<td>30.465</td>
<td>&lt;0.0001</td>
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<td>1352</td>
<td>0.536</td>
<td>0.464</td>
</tr>
<tr>
<td>Treatment x Stress</td>
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<td>&lt;0.0001</td>
<td>2</td>
<td>1352</td>
<td>168.812</td>
<td>&lt;0.0001</td>
</tr>
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<td>0.243</td>
<td>2</td>
<td>43</td>
<td>1.069</td>
<td>0.352</td>
</tr>
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<td>1.989</td>
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<td>2</td>
<td>1352</td>
<td>1.415</td>
<td>0.243</td>
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<td>Treatment x Time</td>
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<td>2</td>
<td>1352</td>
<td>0.278</td>
<td>0.758</td>
</tr>
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<td>Stress x Plant cover</td>
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<td>5.747</td>
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<td>1352</td>
<td>0.34</td>
<td>0.56</td>
</tr>
<tr>
<td>Stress x Month</td>
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<td>1352</td>
<td>4.27</td>
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<td>1</td>
<td>1352</td>
<td>0.876</td>
<td>0.349</td>
</tr>
<tr>
<td>Stress x Time</td>
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<td>0.22</td>
<td>0.639</td>
<td>1</td>
<td>1352</td>
<td>0.876</td>
<td>0.349</td>
</tr>
<tr>
<td>Treatment x Stress x Plant cover</td>
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<td>1352</td>
<td>3.2</td>
<td>0.041</td>
<td>2</td>
<td>1352</td>
<td>3.381</td>
<td>0.034</td>
</tr>
<tr>
<td>Treatment x Stress x Month</td>
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<td>6.094</td>
<td>0.002</td>
<td>2</td>
<td>1352</td>
<td>0.286</td>
<td>0.752</td>
</tr>
<tr>
<td>Treatment x Stress x Time</td>
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<td>1352</td>
<td>5.136</td>
<td>0.006</td>
<td>2</td>
<td>1352</td>
<td>2.019</td>
<td>0.133</td>
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</table>
Table 2. Selection criteria for accelerated failure time (AFT) models of seedling emergence as a function of vegetation treatment (no vegetation, understory vegetation, or overstory vegetation), water and salinity stress gradients, and plant cover for three desert tree species. All models with $\Delta AICc < 4$ are presented and were included in the model averaging of predictions using the Akaike weights ($w_i$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Model rank</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>Model factors*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. glandulosa</em></td>
<td>1</td>
<td>2156.05</td>
<td>0.19</td>
<td>0.19</td>
<td>Treatment + Water stress + Plant cover</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2157.01</td>
<td>0.96</td>
<td>0.12</td>
<td>Treatment + Water stress</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>2157.41</td>
<td>1.36</td>
<td>0.09</td>
<td>Treatment + Water stress + Salinity stress + Plant cover</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>2157.59</td>
<td>1.55</td>
<td>0.09</td>
<td>Treatment x Salinity stress + Water stress + Plant cover</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>2157.72</td>
<td>1.68</td>
<td>0.08</td>
<td>Treatment + Water stress x Plant cover</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>2158.09</td>
<td>2.04</td>
<td>0.07</td>
<td>Treatment + Water stress x Salinity stress + Plant cover</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>2158.37</td>
<td>2.32</td>
<td>0.06</td>
<td>Treatment + Water stress + Salinity stress</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>2158.57</td>
<td>2.52</td>
<td>0.05</td>
<td>Treatment x Salinity stress + Water stress</td>
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<tr>
<td></td>
<td>9</td>
<td>2158.65</td>
<td>2.61</td>
<td>0.05</td>
<td>Treatment + Water stress + Salinity stress x Plant cover</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>2159.00</td>
<td>2.96</td>
<td>0.04</td>
<td>Treatment + Water stress x Plant cover + Salinity stress</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>2159.04</td>
<td>3.00</td>
<td>0.04</td>
<td>Treatment x Plant cover + Water stress</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>2159.05</td>
<td>3.00</td>
<td>0.04</td>
<td>Treatment + Water stress x Salinity stress</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>2159.18</td>
<td>3.13</td>
<td>0.04</td>
<td>Treatment x Salinity stress + Water stress x Plant cover</td>
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<tr>
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<td>14</td>
<td>2159.27</td>
<td>3.22</td>
<td>0.04</td>
<td>Treatment x Water stress + Plant cover</td>
</tr>
<tr>
<td><em>P. pubescens</em></td>
<td>1</td>
<td>1950.30</td>
<td>1</td>
<td></td>
<td>Treatment x Water stress x Plant cover + Water stress x Salinity stress</td>
</tr>
<tr>
<td><em>F. velutina</em></td>
<td>1</td>
<td>7591.12</td>
<td>0.74</td>
<td></td>
<td>Treatment x Salinity stress x Plant cover + Water stress x Salinity stress</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>7593.20</td>
<td>2.08</td>
<td>0.26</td>
<td>Treatment x Salinity stress x Plant cover + Water stress x Plant cover</td>
</tr>
</tbody>
</table>

*Model factors also include the intercept, Weibull scale, and frailty parameters
Table 3. Parameters for model averaged accelerated failure time (AFT) models of seedling emergence for three desert tree species, including parameter relative influence (RI), estimate (Est), and lower and upper 95% confidence intervals (CI). 95% CI not overlapping zero were considered significant (bold). Potential predictor variables included vegetation treatment (no vegetation, understory vegetation [US], and overstory vegetation [OS]), water and salinity stress gradients, plant cover, and interactions between them.

<table>
<thead>
<tr>
<th>Parameter*</th>
<th>P. glandulosa (n = 14 models)</th>
<th>P. pubescens (n = 1 model)</th>
<th>F. velutina (n = 2 models)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment(US)</td>
<td>0.296</td>
<td>-0.026</td>
<td>0.617</td>
</tr>
<tr>
<td>Treatment(OS)</td>
<td>-0.059</td>
<td>-0.371</td>
<td>0.253</td>
</tr>
<tr>
<td>Water stress</td>
<td>1.840</td>
<td>0.778</td>
<td>2.902</td>
</tr>
<tr>
<td>Salinity stress</td>
<td>0.536</td>
<td>0.003</td>
<td>-0.330</td>
</tr>
<tr>
<td>Plant cover</td>
<td>0.730</td>
<td>0.001</td>
<td>-0.009</td>
</tr>
<tr>
<td>Water stress x Salinity stress</td>
<td>0.109</td>
<td>-0.005</td>
<td>-0.017</td>
</tr>
<tr>
<td>Water stress x Plant cover</td>
<td>0.163</td>
<td>-0.002</td>
<td>-0.009</td>
</tr>
<tr>
<td>Salinity stress x Plant cover</td>
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<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Salinity stress x Treatment(US)</td>
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<td>-0.001</td>
<td>-0.004</td>
</tr>
<tr>
<td>Salinity stress x Treatment(OS)</td>
<td>0.179</td>
<td>-0.002</td>
<td>-0.007</td>
</tr>
<tr>
<td>Plant cover x Treatment(US)</td>
<td>0.042</td>
<td>0.000</td>
<td>-0.001</td>
</tr>
<tr>
<td>Plant cover x Treatment(OS)</td>
<td>0.042</td>
<td>0.000</td>
<td>-0.001</td>
</tr>
<tr>
<td>Water stress x Plant cover x Treatment(US)</td>
<td>0.037</td>
<td>-0.035</td>
<td>-0.136</td>
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<tr>
<td>Water stress x Plant cover x Treatment(OS)</td>
<td>0.037</td>
<td>-0.007</td>
<td>-0.090</td>
</tr>
</tbody>
</table>
Table 4. Seedling survival percentage, number of seedlings, and results of log-rank tests comparing Kaplan-Meier estimates of seedling survival for emergent and planted seedlings of three desert tree species under different vegetation treatments.

<table>
<thead>
<tr>
<th>Seedling source</th>
<th>Vegetation treatment</th>
<th>P. glandulosa</th>
<th></th>
<th></th>
<th>P. pubescens</th>
<th></th>
<th></th>
<th>F. velutina</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Survival</td>
<td>N</td>
<td>$\chi^2$</td>
<td>P</td>
<td>Survival</td>
<td>N</td>
<td>$\chi^2$</td>
<td>P</td>
<td>Survival</td>
</tr>
<tr>
<td>Emergent</td>
<td>None</td>
<td>4%</td>
<td>25</td>
<td>3.6</td>
<td>0.163</td>
<td>5%</td>
<td>40</td>
<td>12.9</td>
<td>0.002</td>
<td>8.7%</td>
</tr>
<tr>
<td></td>
<td>Understory</td>
<td>0%</td>
<td>19</td>
<td></td>
<td></td>
<td>0%</td>
<td>12</td>
<td></td>
<td></td>
<td>11.1%</td>
</tr>
<tr>
<td></td>
<td>Overstory</td>
<td>0%</td>
<td>19</td>
<td></td>
<td></td>
<td>8.1%</td>
<td>37</td>
<td></td>
<td></td>
<td>10.0%</td>
</tr>
<tr>
<td>Planted</td>
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<td>55.6%</td>
<td>9</td>
<td>0.8</td>
<td>0.66</td>
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<td>NA</td>
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<td></td>
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<td>59.5%</td>
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<td></td>
<td></td>
<td>58.3%</td>
</tr>
</tbody>
</table>
Table 5. Selection criteria for accelerated failure time (AFT) models of survival of emergent seedlings as a function of vegetation treatment (no vegetation, understory vegetation, or overstory vegetation), water and salinity stress gradients, and plant cover for three desert tree species. All models with $\Delta$AICc < 4 are presented and were included in the model averaging of predictions using the Akaike weights ($w_i$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Model rank</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>Model factors*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. glandulosa</em></td>
<td>1</td>
<td>1048.72</td>
<td>0.41</td>
<td>0.41</td>
<td>Treatment x Water stress x Plant cover + Salinity stress</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1049.87</td>
<td>1.15</td>
<td>0.23</td>
<td>Treatment x Water stress x Plant cover + VSWC x Salinity stress</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1050.33</td>
<td>1.61</td>
<td>0.18</td>
<td>Treatment x Water stress x Plant cover + Salinity stress x Plant cover</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>1051.77</td>
<td>3.05</td>
<td>0.09</td>
<td>Treatment x Water stress x Plant cover + Treatment x Salinity stress</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>1051.98</td>
<td>3.26</td>
<td>0.08</td>
<td>Treatment x Water stress x Plant cover</td>
</tr>
<tr>
<td><em>P. pubescens</em></td>
<td>1</td>
<td>1059.26</td>
<td>0.28</td>
<td>0.28</td>
<td>Water stress x Plant cover</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1059.37</td>
<td>0.12</td>
<td>0.26</td>
<td>Water stress + Plant cover</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1060.46</td>
<td>1.20</td>
<td>0.15</td>
<td>Water stress x Plant cover + Salinity stress</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>1061.61</td>
<td>2.35</td>
<td>0.09</td>
<td>Water stress x Salinity stress + Plant cover</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>1061.80</td>
<td>2.54</td>
<td>0.08</td>
<td>Water stress</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>1062.51</td>
<td>3.25</td>
<td>0.06</td>
<td>Water stress + Salinity stress x Plant cover</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>1063.09</td>
<td>3.83</td>
<td>0.04</td>
<td>Water stress + Salinity stress</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>1063.23</td>
<td>3.97</td>
<td>0.04</td>
<td>Treatment + Water stress x Plant cover</td>
</tr>
<tr>
<td><em>F. velutina</em></td>
<td>1</td>
<td>53704.57</td>
<td>1.00</td>
<td>1.00</td>
<td>Treatment x Water stress + Treatment x Salinity stress x Plant cover</td>
</tr>
</tbody>
</table>

*Model factors also include the intercept, Weibull scale, and frailty parameters as well as covariates for emergent seedling timing and year of seedling emergence.
Table 6. Parameters for model averaged accelerated failure time (AFT) models of survival of emergent seedlings of three desert tree species, including parameter relative influence (RI), estimate (Est), and lower and upper 95% confidence intervals (CI). 95% CI not overlapping zero were considered significant (bold). Predictor variables included vegetation treatment (no vegetation, understory vegetation [US], and overstory vegetation [OS]), water and salinity stress gradients, plant cover, and their interactions.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>P. glandulosa (n = 5 models)</th>
<th>P. pubescens (n = 8 models)</th>
<th>F. velutina (n = 1 model)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RI</td>
<td>Est</td>
<td>Lower CI</td>
</tr>
<tr>
<td>Treatment(US)</td>
<td>1</td>
<td>0.283</td>
<td>-0.733</td>
</tr>
<tr>
<td>Treatment(OS)</td>
<td>1</td>
<td>0.084</td>
<td>-0.879</td>
</tr>
<tr>
<td>Water stress</td>
<td>1</td>
<td>-2.152</td>
<td>-5.828</td>
</tr>
<tr>
<td>Salinity stress</td>
<td>0.919</td>
<td>0.015</td>
<td>-0.009</td>
</tr>
<tr>
<td>Plant cover</td>
<td>1</td>
<td>0.002</td>
<td>-0.012</td>
</tr>
<tr>
<td>Water stress x Salinity stress</td>
<td>0.232</td>
<td>0.019</td>
<td>-0.025</td>
</tr>
<tr>
<td>Water stress x Plant cover</td>
<td>1</td>
<td>0.089</td>
<td>0.035</td>
</tr>
<tr>
<td>Salinity stress x Plant cover</td>
<td>0.185</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Water stress x Treatment(US)</td>
<td>1</td>
<td>4.969</td>
<td>0.577</td>
</tr>
<tr>
<td>Water stress x Treatment(OS)</td>
<td>1</td>
<td>4.517</td>
<td>-0.202</td>
</tr>
<tr>
<td>Salinity stress x Treatment(US)</td>
<td>0.09</td>
<td>0</td>
<td>-0.003</td>
</tr>
<tr>
<td>Salinity stress x Treatment(OS)</td>
<td>0.09</td>
<td>0.001</td>
<td>-0.004</td>
</tr>
</tbody>
</table>
Table 7. Selection criteria for accelerated failure time (AFT) models of survival of planted seedlings as a function of vegetation treatment (no vegetation, understory vegetation, or overstory vegetation), water and salinity stress gradients, and plant cover for *Prosopis glandulosa* and *Fraxinus velutina*. All models with ΔAICc < 4 are presented and were included in the model averaging of predictions using the Akaike weights (w_i).

<table>
<thead>
<tr>
<th>Species</th>
<th>Model rank</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>w_i</th>
<th>Model factors*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. glandulosa</em></td>
<td>1</td>
<td>1764.13</td>
<td>0.43</td>
<td></td>
<td>Water stress x Salinity stress + Plant cover</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1765.29</td>
<td>1.16</td>
<td>0.24</td>
<td>Water stress x Salinity stress</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1766.72</td>
<td>2.59</td>
<td>0.12</td>
<td>Treatment + Water stress x Salinity stress + Plant cover</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>1767.58</td>
<td>3.44</td>
<td>0.08</td>
<td>Water stress x Salinity stress x Plant cover</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>1767.89</td>
<td>3.75</td>
<td>0.07</td>
<td>Treatment + Water stress x Salinity stress</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>1767.90</td>
<td>3.76</td>
<td>0.07</td>
<td>Treatment x Plant cover + Water stress x Salinity stress</td>
</tr>
<tr>
<td><em>F. velutina</em></td>
<td>1</td>
<td>7327.13</td>
<td>0.37</td>
<td></td>
<td>Water stress + Salinity stress x Plant cover</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>7328.93</td>
<td>1.80</td>
<td>0.15</td>
<td>Water stress x Plant cover + Salinity stress</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>7329.37</td>
<td>2.25</td>
<td>0.12</td>
<td>Water stress + Salinity stress</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>7329.39</td>
<td>2.27</td>
<td>0.12</td>
<td>Water stress + Plant cover</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>7330.23</td>
<td>3.10</td>
<td>0.08</td>
<td>Water stress x Salinity stress + Plant cover</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>7330.76</td>
<td>3.63</td>
<td>0.06</td>
<td>Water stress x Plant cover</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>7330.90</td>
<td>3.78</td>
<td>0.06</td>
<td>Treatment + Water stress + Salinity stress x Plant cover</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>7331.01</td>
<td>3.88</td>
<td>0.05</td>
<td>Water stress</td>
</tr>
</tbody>
</table>

*Model factors also include the intercept, Weibull scale, and frailty parameters*
Table 8. Parameters for model averaged accelerated failure time (AFT) models of survival of planted *Prosopis glandulosa* and *Fraxinus velutina* seedlings, including parameter relative influence (RI), estimate (Est), and lower and upper 95% confidence intervals (CI). 95% CI not overlapping zero were considered significant (bold). Potential predictor variables included vegetation treatment (no vegetation, understory vegetation [US], and overstory vegetation [OS]), water and salinity stress gradients, plant cover, and interactions between them.

| Parameter                        |  
|                                  | *P. glandulosa (n = 6 models)* |                                  | *F. velutina (n = 8 models)* |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |                                  |
| (Intercept)                      | RI   | Est   | Lower CI | Upper CI | RI   | Est   | Lower CI | Upper CI | RI   | Est   | Lower CI | Upper CI | RI   | Est   | Lower CI | Upper CI | RI   | Est   | Lower CI | Upper CI | RI   | Est   | Lower CI | Upper CI |
|                                  | 4.988 | 4.541 | 5.435    |          | 5.020 | 4.760 | 5.279    |          |
| Treatment(US)                    | 0.250 | -0.005| -0.077   | 0.067    | 0.056 | -0.003| -0.012   | 0.006    |
| Treatment(OS)                    | 0.250 | 0.065 | -0.078   | 0.209    | 0.056 | -0.002| -0.011   | 0.007    |
| Water stress                     | 1     | 2.201 | 0.422    | 3.981    | 1     | 2.944 | 2.293    | 3.595    |
| Salinity stress                  | 1     | 0.002 | -0.012   | 0.017    | 0.769 | 0.001 | -0.006   | 0.009    |
| Plant cover                      | 0.692 | -0.001| -0.008   | 0.006    | 0.828 | -0.001| -0.006   | 0.003    |
| Water stress x Salinity stress   | 1     | 0.120 | 0.026    | 0.214    | 0.078 | 0.001 | -0.003   | 0.004    |
| Water stress x Plant cover       | 0.077 | -0.001| -0.006   | 0.003    | 0.209 | -0.001| -0.005   | 0.003    |
| Salinity stress x Plant cover    | 0.077 | 0.000 | 0.000    | 0.000    | 0.423 | 0.000 | 0.000    | 0.000    |
| Plant cover x Treatment(US)      | 0.066 | 0.000 | -0.001   | 0.001    |        |        |          |          |
| Plant cover x Treatment(OS)      | 0.066 | -0.001| -0.003   | 0.001    |        |        |          |          |
| Water stress x Salinity stress x Plant cover | 0.077 | 0.000 | 0.000    | 0.000    |        |        |          |          |
Figure 1. Relationship between the water stress (measured as volumetric soil water content) and salinity stress gradients (measured as electrical conductivity) with marginal frequency distributions of each gradient.
Figure 2. (a) Difference (±SE) and percent difference in volumetric soil water content (VSWC) associated with understory and overstory vegetation treatments compared to the no vegetation treatment along the water stress gradient. (b) Difference (±SE) and percent difference in electrical conductivity (EC) associated with understory and overstory vegetation treatments compared to the no vegetation treatment along the salinity stress gradient. Stress gradient values were binned for clarity.
Figure 3. Predicted effects of the interactions between vegetation treatment, water stress gradient, and the variables (a) plant cover, (b) sampling month, and (c) time since the beginning of the experiment on volumetric soil water content (VSWC). The gray line indicates the baseline relationship (1:1) for subplots without vegetation and the other lines indicate the relationship between VSWC and its gradient at the minimum (dotted), mean (solid), and maximum (dashed) values of the variable in that panel.
**Figure 4.** Predicted effect of the interaction between vegetation treatment, salinity stress gradient, and plant cover on electrical conductivity (EC). The gray line indicates the baseline relationship (1:1) for subplots without vegetation and the other lines indicate the relationship between EC and its gradient at the minimum (dotted), mean (solid), and maximum (dashed) values plant cover.
Figure 5. Mean (±SE) total emergence percentage for seeds of three desert tree species planted in three vegetation treatments in relation to water and salinity stress gradients.

Missing levels had zero emergence. Stress gradient values were binned for clarity.
Figure 6. Relative risk of *Prosopis glandulosa* seedling emergence, death of emergent seedlings, and death of planted seedlings in the understory vegetation treatment compared to the no vegetation treatment along the water stress gradient. Width of the line represents the range of relative risk after taking the effects of electrical conductivity into account. Relative risk above the dotted line at zero indicates that emergence or death is greater in the understory vegetation treatment than in the no vegetation treatment, with the converse holding below the zero line. Plant cover is modeled as a continuous variable, but represented by five categories in this figure to demonstrate the effects of its interactions with other variables.
Figure 7. Relative risk of *Prosopis glandulosa* seedling emergence, death of emergent seedlings, and death of planted seedlings in the overstory vegetation treatment compared to the no vegetation treatment along the water stress gradient. Lines represent the effects of interactions with the salinity stress gradient (range of values: 1 dS m\(^{-1}\) to 75 dS m\(^{-1}\)). Relative risk above the dotted line at zero indicates that emergence or death is greater in the overstory vegetation treatment than in the no vegetation treatment, with the converse holding below the zero line. Plant cover is modeled as a continuous variable, but represented by five categories in this figure to demonstrate the effects of its interactions with other variables.
Figure 8. Relative risk of *Prosopis pubescens* seedling emergence in the understory and overstory vegetation treatments compared to the no vegetation treatment along the water stress gradient. Relative risk above the dotted line at zero indicates that emergence is greater in the understory or overstory vegetation treatment than in the no vegetation treatment, with the converse holding below the zero line. Plant cover is modeled as a continuous variable, but represented by five categories in this figure to demonstrate the effects of its interactions with other variables.
Figure 9. Relative risk of *Fraxinus velutina* seedling emergence, death of emergent seedlings, and death of planted seedlings in the understory vegetation treatment compared to the no vegetation treatment along the salinity stress gradient. Lines represent the effects of interactions with the water stress gradient (range of values: 0.01 to 0.73). Relative risk above the dotted line at zero indicates that emergence or death is greater in the understory vegetation treatment than in the no vegetation treatment, with the converse holding below the zero line. Plant cover is modeled as a continuous variable, but represented by five categories in this figure to demonstrate the effects of its interactions with other variables.
**Figure 10.** Relative risk of *Fraxinus velutina* seedling emergence, death of emergent seedlings, and death of planted seedlings in the overstory vegetation treatment compared to the no vegetation treatment along the salinity stress gradient. Lines represent the effects of interactions with the water stress gradient (range of values: 0.01 to 0.73). Relative risk above the dotted line at zero indicates that emergence or death is greater in the overstory vegetation treatment than in the no vegetation treatment, with the converse holding below the zero line. Plant cover is modeled as a continuous variable, but represented by five categories in this figure to demonstrate the effects of its interactions with other variables.
Figure 11. Survival percentage for emergent and planted seedlings of three desert tree species planted in three vegetation treatments in relation to the water stress gradient. Stress gradient values were binned for clarity.
Figure 12. Survival percentage for emergent and planted seedlings of three desert tree species planted in three vegetation treatments in relation to the salinity stress gradient. Stress gradient values were binned for clarity.
CHAPTER 4. COMPETITIVE INTERACTIONS BETWEEN TREES VARY AT LOCAL SCALES IN SAVANNAS: EVIDENCE FROM POINT PATTERN ANALYSIS OF REMOTELY SENSED DATA

ABSTRACT

The spatial distribution of plants is often interpreted as an indicator of underlying abiotic and biotic processes. In arid ecosystems, questions of interest are the extent to which competition structures the spatial pattern of woody species, whether the importance of these plant interactions varies with the abiotic environment, and at what scales. Here, I analyzed tree spatial patterns in a groundwater-driven savanna using local indicators of spatial association and nearest neighbor analyses to examine spatial variation in tree interactions. I first developed a regional map of tree locations using object-based classification of high resolution multispectral imagery and LiDAR spatial data. This classification process resulted in relatively accurate delineation of trees > 2-m tall, except in dense woodland situations. The analysis of the resulting point patterns strongly supported the importance of competition in shaping tree distributions at both local and global scales. Local pair correlation functions showed an increase in the regularity of spatial patterns, suggestive of competition, associated with increasing tree height and distance from surface water. Nearest neighbor analysis showed a positive association between mean distance to and height of the four nearest neighbors within clusters of large trees, indicating potential density-dependent mortality associated with competition. Distance to surface water was positively associated with the magnitude of the tree height-distance relationship. In both analyses, there was an increase in the magnitude of evidence of competition with tree size indicative of accumulation of
competitive effects over time. These findings highlight the utility of remote sensing and object-based classification for development of large spatial datasets of tree distributions as well as the utility of local point pattern analysis for examining spatio-temporal variation in the importance and effects of plant interactions.

INTRODUCTION

The causes and consequences of spatial patterns of plants in natural communities remains an important topic in ecology (Levin 1992). Spatial structuring of plants results from dispersal, facilitation, and mortality due to abiotic stress, disturbance, and competition. In arid ecosystems, there has long been interest in the extent to which competition structures the spatial pattern of woody species at small scales (Fonteyn and Mahall 1981; Phillips and MacMahon 1981; Fowler 1986; Scholes and Walker 1993). The presence and extent of competitive interactions between plants can be inferred from the spatial distribution of individuals within a community (Pielou 1962; Phillips and MacMahon 1981; Fowler 1986). Regular spatial patterns are frequently interpreted as a sign of intense competition for limited resources among plants, while aggregated and random patterns can result from a variety of processes (Phillips and MacMahon 1981; Archer et al. 1988; Schurr et al. 2004). Theoretically, equal spacing relative to resource availability should provide optimal growth for all individuals, with this regularity resulting from competition between nearby individuals and subsequent density-dependent mortality (Dwyer et al. 2010). In arid savanna ecosystems, self-thinning associated with competitive interactions is a potential mechanism of stabilization of woody vegetation density in a patch-dynamic pattern (Wiegand et al. 2006; Sea and Hanan 2012). However,
The analysis of tree spatial patterns in savannas has inconsistently supported the importance of competitive plant interactions (Shackleton 2002; Schurr et al. 2004; Moustakas et al. 2008).

Because various processes can create the same spatial pattern or produce patterns that can be indistinguishable from complete spatial randomness (CSR; Levin 1992; Molofsky et al. 2002; Perry et al. 2006), it can be difficult to directly infer process from spatial pattern. McIntire and Fajardo (2009) suggest that differentiating the effects of multiple processes on spatial pattern formation relies on precise spatial analysis and several strong alternative *a priori* hypotheses. Precise spatial analysis necessitates effective spatial analysis methods and accurate spatial location data (Freeman and Ford 2002), which can be time consuming to gather and inconsistent in spatial reference using field methods. Alternatively, remote sensing of tree location and size provides a spatially consistent reference for tree location data and, if utilizing LiDAR, analysis of forest and individual tree structure (e.g., McCombs et al. 2003; Popescu and Wynne 2004; Coops et al. 2004; Levick and Rogers 2006; Richardson and Moskal 2011; Colgan et al. 2012). Explicit hypotheses and predictions are advisable to direct focus to the biological question and avoid data dredging (Schurr et al. 2004).

The majority of studies analyzing point patterns in search of plant interactions have assumed that the effects of plant interactions are spatially invariant within study sites (but see Barot et al. 1999; Barot and Gignoux 2003; Lancaster and Downes 2004; Law et al. 2009; Dwyer et al. 2010). This assumption is clearly in conflict with the complexity inherent in natural systems and contrary to the central premise of landscape ecology, that pattern-process relationships are variable across spatial and temporal scales.
Arid ecosystems exhibit strong local heterogeneity in which the relationship between spatial pattern and process is likely non-stationary. In particular, competitive interactions between woody plants have frequently been found to vary with underlying gradients in environmental stress, especially stress associated with water (Maestre et al. 2005; Wiegand et al. 2006). The stress gradient hypothesis predicts that the intensity and importance of competitive interactions will be inversely related to environmental stress (Bertness and Callaway 1994). Conversely, there has also been support for a positive association between tree competition and high environmental stress in savannas (Dwyer et al. 2010). There have been conflicting results in the few examinations of variation between sites with different water availabilities in the second-order statistics of point patterns, which examine interactions between trees (e.g., Shackleton 2002; Belay and Moe 2012). However, competitive interactions occur between individuals at local scales, which these aggregated, global analysis approaches at larger scales may not be able to capture. In general, global analysis can be very misleading at local scales if there is spatial variation in these relationships (Lancaster and Downes 2004; Law et al. 2009), as is expected for competitive interactions. As an alternative to global analysis, local point pattern analysis captures this spatial variation and provides a “plant’s eye view” (Fotheringham 1997; Perry et al. 2006).

The objective of this study was to investigate the prevalence of competitive interactions among trees in an arid savanna in relation to water stress gradients. I developed a tree spatial location dataset using remotely sensed data, ensuring a common spatial precision to better detect spatial associations at small scales, and evaluated the adequacy of the dataset. Then, I developed the following set of predictions in line with
the hypothesis that competition is a major driver of local spatial patterns of trees. If mortality is associated with competition, I predict: (1) there will be localized evidence of regularity at distances up to 40 m from each tree, corresponding to a maximum recorded rooting radius of 20 m as generally found for tree species related to those at Ash Meadows (Stone and Kalisz 1991); (2) localized regularity will increase with tree size as competition-related mortality accumulates over time; and (3) there will be strong, localized positive associations between tree size and distance to the nearest neighbor. If the frequency and intensity of plant interactions are associated with water stress, I expect support for these predictions to vary with distance to surface water and thus only local, not global, statistics to elucidate these patterns.

**METHODS**

**Study area**

Ash Meadows National Wildlife Refuge is located in the Amargosa Valley, NV, in the northern Mojave Desert, approximately 145 km northwest of Last Vegas, NV, and 64 km east of Death Valley National Park. Average high temperatures are 40°C in summer, average low temperatures are -1°C in winter, and average annual precipitation is 10 cm. The primary source of water for vegetation is groundwater, which discharges from over 30 springs and seeps in the 9310-ha refuge (Otis Bay and Stevens Ecological Consulting 2006). Vegetation types vary in relation to water availability, ranging from emergent wetlands (*Typha* spp., *Scirpus* spp., *Eleocharis* spp., and *Carex* spp.) where surface water is present to sparsely vegetated alkali and desert scrub (*Atriplex* spp., *Isocoma acradenia*, *Lycium* spp., *Larrea tridentata* [DC.] Cov.). Savannas occur between
these two extremes and contain a mixture of grass (*Carex* spp., *Juncus* spp., *Distichlis spicata*, *Sporobolus airoides*) and trees (*Salix* spp., *Tamarix* spp., *Fraxinus velutina* Torr., *Prosopis pubescens* Benth., *P. glandulosa* Torr. var. *torreyana*). There was extensive mechanical and herbicide-based management of the invasive exotic *Tamarix* in the study area from 2006 – 2008.

**Image data and preprocessing**

I produced a 0.6-m multispectral image by using the Gram-Schmidt method (ENVI 4.3; Exelis Visual Information Solutions, Boulder, CO, USA), which is robust to both unsupervised and supervised classifications (Du and King 2007), to pan sharpen orthorectified QuickBird imagery obtained 28 August 2004 (Spatial Solutions, Inc., Bend, OR, USA). Pan sharpening integrates a higher resolution panchromatic image (0.6-m resolution) with a lower resolution multispectral image (2.4-m resolution) to generate a higher resolution multispectral image. Although this method does not preserve the original image radiance values, it is commonly used because it increases the ability to extract small features (e.g., trees or bare patches between trees) that are only present in the panchromatic image (Wald et al. 1997). The soil adjusted vegetation index (SAVI) was derived using a soil-adjustment factor of 0.5, a proxy for vegetation abundance commonly used in sparsely vegetated areas, from the pan-sharpened near-infrared and red light spectral bands (Huete 1988).

For canopy height, I used surface and bare ground digital terrain models of orthorectified 0.33-m LiDAR data (White Horse Associates Inc. 2008) to derive a normalized digital surface model (nDSM). I then calculated slope from the nDSM to help
detect canopy edges. Surface water features (springs, reservoirs, streams, and impoundments) were hand-digitized from the QuickBird imagery and water availability was represented as Euclidean distance to surface water.

**Image classification**

I used an object-based multiresolution image analysis method to segment images into patches and classify patches as tree or non-tree in the software eCognition Developer. (ver. 8.8; Trimble 2012). Object-based classification uses spectral (e.g., radiance, color) and spatial (e.g., size, shape, texture, and adjacency) information to segment imagery into objects and assign objects to classes with similar characteristics. This classification method has been successfully used to identify shrubs and trees in other arid ecosystems and represents a substantial improvement over pixel-based analyses (e.g., Thomas et al. 2003; Laliberte et al. 2007). Inclusion of both high resolution spectral and LiDAR surface elevation data in object-based image analysis allows for the further extraction of tree height and canopy dimensions.

Segmentation in eCognition occurs through a bottom-up, region-merging algorithm in which smaller image objects are merged into larger ones based on the increase in heterogeneity between adjacent objects. I initially segmented objects according to surface elevation (nDSM) to find objects of relatively homogenous vegetation height. In the eCognition segmentation process, the scale parameter defines the minimum size of image objects relative to the image resolution, so a larger scale parameter results in larger objects. I parameterized scale to account for the minimum identifiable woody plant area (scale = 1). Object homogeneity is managed by mutually
exclusive interactions between color (the spectral response of objects) and shape (textural characteristics of objects) weighting factors, with shape further defined by smoothness and compactness. I calibrated these parameters using an ad hoc, iterative procedure and visual assessment, resulting in color/shape = 0.8/0.2 and smoothness/compactness = 0.2/0.8.

I used user-defined thresholds to classify initial image objects as tree or non-tree based on training data collected in the field. Thresholds of a minimum canopy height ≥ 1 m and SAVI ≥ 0 extracted objects with substantial vegetation cover. I separated trees from tall grasses (e.g., Typha and Phragmites spp.) by re-segmenting vegetated areas at a larger scale (scale = 10) and using nearest neighbor classification on samples of tree and non-tree vegetation. Nearest neighborhood classification is based on a fuzzy classification algorithm in which classified image objects have membership values ranging from zero to one for each class based on the difference in feature space between the object to be classified and the training data for that class. Unclassified or wrongly classified objects are assigned to the correct class by adding more training data in an iterative fashion, presumably leading to greater accuracy. I used textural heterogeneity of the DSM and the slope of nDSM of the sub-objects (i.e., the initial scale = 1 objects) to separate trees (high heterogeneity) from other tall vegetation (low heterogeneity).

After extracting tree cover, I delineated individual tree crowns. First, I re-segmented tree-covered areas at the pixel scale. Then, I classified canopy edges based on their proximity to non-vegetated areas or by the maximum local extrema in the ratio of nDSM to the slope of nDSM. This ratio is larger where trees are shorter and the slope of their canopies is steeper and helped identify tree edges between adjacent trees. Tree
centers were classified using local minima of the same nDSM: slope of nDSM ratio. I then iteratively added to these tree centers based on minimum differences in nDSM and SAVI until tree edges were reached. After tree crowns were delineated, tree height was extracted as the maximal pixel value in each object. I did not directly assess tree canopy area because the multispectral imagery and LiDAR data were from different timeframes, meaning that the edges of canopies differed between them. Maximal tree height is generally near the center of a tree, so this mismatch in edges would not lead to the same bias for tree height. For the purpose of point pattern analysis, I described the location of each tree in geographic space as occurring in the center of each object.

Training and testing data were collected at 172 30- x 30-m sites located randomly in areas where trees could occur (i.e., not on mountain slopes or in water) in 2008 through 2011 at Ash Meadows. At each site, I mapped the spatial location of each tree and recorded its species, height, and crown diameter along the major and minor axes. I recorded 4712 trees, of which 3649 had canopy diameters of at least 1.2 m (twice the pixel resolution for the pan-sharpened QuickBird imagery) and thus had a possibility of being detected. Half of the mapped trees were used as training data for classification and the remaining half of the data was used for accuracy assessment.

The accuracy of the tree map was assessed on three levels: tree cover, presence/absence of individual trees, and size of individual trees. For tree cover, I calculated Pearson’s correlation coefficient between tree cover derived from the object-based classification and from field data. For presence/absence of individual trees, I determined the number of correctly detected trees, falsely detected trees, and falsely undetected trees for trees with canopies <2 m², 2-5 m², 5-10 m², and >10 m² in the
testing data. Trees were considered detected if the modeled tree canopy overlapped the field-mapped tree point. From the contingency table, I calculated producer’s (omission error), user’s (commission error), and overall accuracy as well as the kappa statistic, a measure of accuracy that corrects for chance. To estimate the validity of tree size derived from object-based analysis, I calculated Pearson’s correlation coefficient between modeled and field-measured tree height.

**Point pattern analysis**

To examine spatial variation in the association between trees at local scales, I used a complementary combination of local variations of global univariate statistics. I used local statistics because global statistics contribute little meaningful information when spatial patterns do not exhibit either first- or second-order reweighted stationarity across a region (Fotheringham 1997). I was particularly interested in the within-region spatial variation and therefore used local indicators of spatial association (LISA; Anselin 1995) and nearest neighbor analysis (Pielou 1962). Local analysis can detect local associations around individuals, highlighting clusters of aggregation or high values (hot spots) from clusters of regularity or low values (cold spots) across a region (Anselin 1995). LISA methods are less effective when the intensity of competition is insufficient to result in differential mortality, but nearest neighbor statistics can detect weaker competitive effects that manifest in differences in tree size with distance, helping differentiate between the importance and intensity of competition (Welden and Slauson 1986). All analyses were conducted at distances up to 40 m in light of the likely rooting
extent of trees (Stone and Kalisz 1991) and edge effects were avoided by not analyzing trees within 40 m of the study area border.

I used a LISA function based on the pair correlation function ($g(r)$; Stoyan and Stoyan 1994) to evaluate if significant tree interactions occur at specific scales. The pair correlation function measures the density of trees within a ring at a particular distance $r$ from the focal tree. Although closely related to Ripley’s $K$ (Ripley 1977), it is non-cumulative and consequently allows identification of specific scales at which tree interactions occur. I used the inhomogeneous form of the function which weights each tree by the inverse of intensity at that location because intensity was not stationary across the study area. To assess the significance of global and local $g(r)$, I computed 95% confidence envelopes from 99 Monte Carlo simulations of the inhomogeneous Poisson process. Values of $g(r)$ greater than the confidence envelope reveal significant aggregation and values less than the confidence envelope reveal significant regularity. As a LISA, global $g(r)$ is proportional to the sum of all local $g(r)$. I used the local test statistic to identify the frequency and extent of significant deviations (±2 SD) across the set of distances $r = 0$ to 40 m (prediction 1).

I calculated two nearest-neighbor indices based on distance to the nearest four neighbors and all neighbors within the 40-m maximum tree interaction extent. For the nearest four neighbors, I calculated the average distance to the center point of the nearest four neighbors for each tree (an estimate of clumping or regularity) and the mean height of the four nearest neighbors and focal tree. I used more than one neighbor to help avoid bias associated with the nearest tree not being the major competitor due to size or species
Nearest neighbor analyses are density dependent, and thus may be biased by non-stationarity in point pattern intensity.

**Analysis of local tree interactions**

I used the Getis-Ord G-star statistic \( G_i^* \) (Getis and Ord 1992) to identify clusters of tall and short trees. Tree height was significantly, positively correlated with canopy area in field data \( (r = 0.75) \) and is likely correlated with rooting extent. The \( G_i^* \) statistic measures the concentration of small or large trees within distance \( r \) of each tree and then classifies that focal tree as a non-member of a cluster or member of a cluster of large or small trees (Anselin 1995). Significance was assessed using 999 Monte Carlo simulations of a random permutation test.

I used clusters of large and small trees to evaluate whether patterns of local \( g(r) \) varied with tree size in line with prediction (2). I explored the effects of water availability on local \( g(r) \) using a generalized linear model (GLM). Like all parametric statistics, GLMs assume independence between data points. I performed a bootstrap analysis using 99 random subsets of 20% of the data to reduce the effects of spatial autocorrelation in interpreting model parameters averaged across bootstrap iterations.

I analyzed the correlation between the mean height and mean distance of the four nearest neighbors around each focal tree to examine the correlation between tree size and nearest neighbor distances (prediction 3). I also examined whether there were differences in this relationship with focal tree size or between clusters of large and small trees based on significant \( G_i^* \) using a GLM. The GLM included interactions between mean nearest neighbor distance, focal tree size, and type of cluster or non-cluster membership. To
determine if the size-distance relationship varied with water availability, I included
distance to surface water as an additional interactive variable in the model and tested for
significance using the $F$-test.

**RESULTS**

**Tree classification**

Object-oriented classification resulted in delineation of 225,637 trees ≥ 2-m
height (Fig. 1). The LiDAR-derived nDSM and slope of the nDSM data rather than the
multispectral imagery appeared to drive the delineation of individual tree canopies (Fig.
2). Tree cover resulting from the object-based classification was highly correlated with
that derived from field estimates ($r = 0.86$), but was slightly underestimated due to
exclusion of the outer edges of tree objects (Fig. 3). Tree heights for trees > 2m tall were
comparable for LiDAR-derived estimates and field data ($r = 0.89$), although
underestimated for smaller trees.

I found moderate overall agreement in the delineation of trees between object-
based classification and field-collected testing data, with accurate detection increasing
substantially for larger trees (Table 1). Although the smallest detectable trees were > 2 m
in height, this class of trees was not consistently detectable because trees were generally
only two pixels wide. This small object area combined with the small stature and low
SAVI of smaller trees likely limited detection. A minimum width of three pixels appeared
to mitigate this issue. I excluded this size class from further analysis based on its low
detectability, and its exclusion increased overall accuracy to 0.73 and the kappa index to
0.57.
For larger size classes, undetected trees (errors of omission) are primarily the result of insufficient object segmentation in woodland areas with heavy cover (Fig. 3). Although the edges of trees were visually distinct because of their relatively spherical shape, there was little difference in nDSM, the slope of nDSM, or multispectral characteristics between trees for the object-based classification to exploit.

**Point pattern analysis of tree interactions**

The spatial pattern of trees was inhomogeneous at the landscape scale (Fig. 1) and was significantly related to water availability. Inhomogeneous global $g(r)$, which accounted for the non-stationarity in tree intensity, was near zero across distances $r = 0$ to 40, indicating a significantly regular distribution of tree interactions at the landscape scale suggestive of net competition. At the local scale, there was more variation in $g(r)$, with significant clumping occurring around a minority of trees at $r \leq 10$ m and a shift to greater regularity with increasing distance $r$ (Figs. 4 and 5). The majority of local $g(r)$, regardless of distance $r$, exhibited a regular pattern. Local $g(r)$ was negatively associated with height of the focal tree ($\beta \pm SE = -6.05 \times 10^{-4} \pm 9.04 \times 10^{-5}$) and significant clumping at short distances was associated with shorter focal trees (Fig. 4). There was no difference in the frequency of significant clumping or regularity within clusters of small or large trees, but the magnitude of local $g(r)$ was greater in clusters of large trees. Distance to surface water was significantly, negatively related to local $g(r)$ within $r \leq 40$ ($\beta \pm SE = -1.64 \times 10^{-7} \pm 1.49 \times 10^{-7}$; Fig. 4).

Results for the relationship between mean height and distance of the nearest four neighbors varied in relation to the size of focal trees and membership in clusters of large
and small trees (Table 2). At the global scale, there was a weak, negative relationship between nearest neighbor height and distance \((r = -0.024; P < 0.001)\). At local scales, the direction of the relationship was strongly associated with tree height and differed between clusters of different tree sizes (Table 2; Fig. 6). Within clusters of small trees, there was a significant negative relationship between nearest neighbor distance and height \((r = -0.25;\) Fig. 6). Conversely, a significant positive size-distance relationship occurred within clusters of large trees \((r = 0.18;\) Fig. 6). Inclusion of an interactive effect of distance to surface water had a significant, but very small, positive effect on this relationship (four-way interaction term: \(F = 8.03, P = <0.001\)), with a greater increase in height with distance from nearest neighbor in clusters of large trees than in clusters of small trees.

**DISCUSSION**

**Object-based classification**

Overall classification was of comparable accuracy to those found in other studies in arid environments (e.g., Laliberte et al. 2007; Colgan et al. 2012), but less accurate than those achieved for coniferous forests with conical tree crowns (e.g., McCombs et al. 2003; Coops et al. 2004; Richardson and Moskal 2011). I found that accuracy varied with tree size (Table 1) and suggest that the minimum detectable tree needs to be at least three pixels wide. My results corroborate those of Richardson and Moskal (2011), who found that the Individual Tree Canopy (ITC) method, which is similar to the object-oriented method described here, also underestimated density of small trees, particularly those beneath the canopies of other trees.
For errors associated with larger trees in this classification, trees appeared to be detected, but not delineated, in closed canopy situations where edges of objects are difficult to detect (Fig. 2). Trees at Ash Meadows tended to have flat canopies limiting the utility of algorithms that delineate adjacent trees by identifying local canopy height maxima and minima, including tree seed and watershed-based algorithms. Although canopy edges were visually identifiable, I was unable to translate this identification into an automated rule set to delineate individual trees. Considering that there is likely greater potential for competition where trees are denser, this may have substantially biased the point pattern analysis of tree interactions to not detect localized clumping of trees in woodlands.

I found that LiDAR-estimated tree height for trees > 2 m was lower, but strongly related to field measurements, as have other studies in a variety of ecosystems (e.g., McCombs et al. 2003; Popescu and Wynne 2004; Coops et al. 2004; Levick and Rogers 2006). The high correlation between measurements suggests that LiDAR is a sufficiently accurate method for determining the height of individual trees for use in spatial statistics. Although there is error associated with both LiDAR- and field-based measurements, the consistency of the direction of the error suggests LiDAR is the primary source. This is a common problem because small-footprint LiDAR may not always penetrate or interact with the top of the crown (Roberts et al. 2007). In addition, although field sampling for testing data began in 2008 when the LiDAR was flown, sampling continued for three years and tree heights are likely to have increased over the sampling interval. However, there was no significant effect of year in a regression model of LiDAR- versus field-derived tree height ($\beta\pm SE = 0.027\pm0.041$).
Although the methods need further refinement, my approach has potential for
development of large-scale tree datasets for point pattern analysis, particularly with ever-
increasing resolution and accuracy of spatial data. Collecting spatially accurate tree data
is time consuming using traditional field methods, but quick with remote sensing and
image classification. Remote sensing would also allow for repeated sampling using the
same methods, allowing the tracking of point patterns and plant interactions over time
and space. The analysis here suggests that valid results are limited to trees > 2-m tall and
to trees located in less dense woodlands. Further refinement of the object-based
classification to delineate adjacent trees in dense conditions would significantly reduce
this limitation.

Tree interactions

Tree density was significantly related to water availability (Fig. 1), as would be
expected in an arid environment (e.g., Fensham et al. 2005; Sankaran et al. 2008). Ash
Meadows is groundwater-driven and is of small spatial extent, but these patterns and the
importance of water are consistent with results for tree cover across a large scale
precipitation gradient in Africa (Sankaran et al. 2008), suggesting the general importance
of water in limiting both plant regeneration (Chapters 2 and 3) and spatial distributions
(Chapter 4).

Both $g(r)$ and nearest neighbor analyses provided strong evidence for the
importance of competitive interactions between trees. These results likely have a bias
towards finding regularity due to poor delineation of some adjacent trees in dense
woodlands during the object-oriented classification. However, there was strong evidence
of competition across a range of local distances, densities, and tree sizes, suggesting these results are not an artifact of the classification process. Results are consistent with those from several other savanna systems and provide further evidence that competitive interactions can lead to density-dependent mortality (e.g., Meyer et al. 2008; Moustakas et al. 2008; Sea and Hanan 2012; Belay and Moe 2012), which may contribute to the maintenance of the savanna dynamic (Wiegand et al. 2006; Sea and Hanan 2012). The significant regularity evident in global and local $g(r)$ up to $r = 40$ m pointed to the dominance of competition within the distance of likely plant interactions. Local analysis provided a deeper understanding of the likely spatio-temporal dynamics in plant interactions, showing that regular, clumped, and random patterns of tree interactions can occur at local scales depending on the size of focal trees and distance to surface water (Figs. 4 and 5). This spatial variation in plant interactions was not reflected in global statistics.

Nearest neighbor analyses provided a complementary analysis of the effects of competitive interactions on size in relation to density. Nearest neighbor analysis at local scales revealed a significant negative relationship between distance and tree height in clusters of small trees and a significant positive relationship between distance and tree height in clusters of large trees (Fig. 5). The positive relationship for larger trees and the shift in relationship with tree size were in line with my predictions regarding the importance of competitive interactions. The negative relationship found for smaller trees suggests the importance of dispersal patterns or facilitation in earlier life stages (see Chapter 3). In contrast to $g(r)$, global analysis of nearest neighbor relationships did not
support the importance of competitive interactions, primarily due to the dominance of smaller trees, and masked this significant shift with tree size.

Local $g(r)$ and nearest neighbor analysis also supported the importance of other biotic processes, particularly dispersal and facilitation, and the abiotic environment in shaping tree distributions (e.g., Shackleton 2002; Schurr et al. 2004). The evidence of clumping of smaller trees at small spatial scales may have resulted from short-distance dispersal and spatial variation in microsites (Schurr et al. 2004). All of the dominant tree species at Ash Meadows have dispersal syndromes that could lead to clumped trees. A major dispersal agent of *Prosopis glandulosa* and *P. pubescens* is coyote endozoochory, with local seed dispersal spatially autocorrelated due to deposition of many seeds within feces and due to coyote habitat selection (Chapter 1). *Fraxinus velutina* is wind-dispersed, with the majority of seeds falling within 5 m of the mother tree (unpubl. data). Likewise, dispersal of all dominant trees is directed towards what is likely suitable habitat because of autocorrelation between seed dispersal and the presence of existing trees (Chapter 1). The negative relationship between nearest neighbor distance and height for small trees may be indicative of facilitation between trees, suggesting synergy between clumped seedling emergence and facilitation may foster seedling establishment (Chapter 3). The shift to a positive relationship between nearest neighbor distance and height with increasing tree size is consistent with studies in other savanna systems and strong evidence for density-dependent self-thinning processes induced by competition (Meyer et al. 2008; Belay and Moe 2012).

I found a small, significant negative effect of distance to surface water on local $g(r)$ (Fig. 5) and a small, significant positive effect on the size-distance relationship
between nearest neighbors (Table 2). Both local \( g(r) \) and nearest neighbor analyses suggest that competition is more important where there is less water available. This relationship between water availability and nearest neighbor analysis contrasts with the results of Shackleton (2002), who found that sites with evidence of competition tended to have greater annual rainfall at the regional scale in African savannas. The effect found in this study could be an artifact of the chosen water availability measure not adequately capturing spatial and temporal variation in water availability or an artifact of the underestimation of tree density in dense woodlands, which tend to be located near surface water. Alternatively, an ecological relationship could explain the results. One possibility is that the more stable interannual and seasonal groundwater dynamics at Ash Meadows do not lead to the same extent of drought-induced mortality as in other arid ecosystems (Fensham et al. 2009; Dwyer et al. 2010). Fensham et al. (2009) drew a distinction between mesic and xeric savannas driven by precipitation, suggesting that trees do not exhaust deep soil moisture where there is reliable precipitation. My results in a groundwater-driven system support this interpretation of the importance of water to plant competition.

**CONCLUSIONS**

Remote sensing and object-based classification methods for delineating tree crowns provide the means to analyze point patterns across broad spatial scales. Interpretation of the results should be cautioned by the accuracy of the classification; in particular, results suggest that analysis should be restricted to trees captured in imagery as larger than three data pixels wide. Point pattern analysis at a regional scale showed that
assumptions of first- and second-order homogeneity and stationarity were clearly violated at Ash Meadows, as is likely in all ecosystems at some scale. These assumptions limit ecological understanding because heterogeneity gives rise to different processes (e.g., competition or facilitation) in different locations. Studies of the spatial pattern-process relationship in other arid savanna ecosystems support this need for the direct consideration of heterogeneity across a variety of scales (Shackleton 2002; Levick and Rogers 2011). Although I accounted for first-order non-stationarity through use of inhomogeneous point pattern processes, results clearly showed that global statistics mask local second-order heterogeneity and thus obscured pattern-process relationship. This calls into question interpretation of global statistics, even based on inhomogeneous Poisson processes, for analyzing processes that occur at local scales.

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REFERENCES


**Table 1.** Contingency table and accuracy assessment results for the object-based classification of individual trees by size class.

<table>
<thead>
<tr>
<th>Classification data</th>
<th>&lt; 2 m²</th>
<th>2 - 5 m²</th>
<th>5 - 10 m²</th>
<th>&gt;10 m²</th>
<th>No tree</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree &lt; 2 m²</td>
<td>209</td>
<td>18</td>
<td>1</td>
<td>0</td>
<td>76</td>
</tr>
<tr>
<td>Tree 2 - 5 m²</td>
<td>4</td>
<td>1556</td>
<td>21</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>Tree 5 - 10 m²</td>
<td>0</td>
<td>105</td>
<td>529</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Tree &gt;10 m²</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>No tree</td>
<td>572</td>
<td>597</td>
<td>27</td>
<td>0</td>
<td>0</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Testing data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Producer's accuracy</td>
<td>0.27</td>
</tr>
<tr>
<td>User's accuracy</td>
<td>0.69</td>
</tr>
<tr>
<td>Overall accuracy</td>
<td>0.62</td>
</tr>
<tr>
<td>Kappa index</td>
<td>0.44</td>
</tr>
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</table>
Table 2. ANOVA results summarizing the generalized linear model of the relationship between mean height and mean distance of the four nearest neighbors (NN) and covariates representing height of the focal tree and membership or non-membership in clusters of large or small trees derived using $G_i^*$. 

<table>
<thead>
<tr>
<th>Predictor</th>
<th>df</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>NN distance</td>
<td>1</td>
<td>3678</td>
<td>3678</td>
<td>1616</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Tree height</td>
<td>1</td>
<td>585031</td>
<td>585031</td>
<td>257100</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cluster membership</td>
<td>2</td>
<td>217528</td>
<td>108764</td>
<td>47800</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>NN distance x Tree height</td>
<td>1</td>
<td>10</td>
<td>10</td>
<td>4.193</td>
<td>0.041</td>
</tr>
<tr>
<td>NN distance x Cluster membership</td>
<td>2</td>
<td>8555</td>
<td>4277</td>
<td>1880</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Tree height x Cluster membership</td>
<td>2</td>
<td>4383</td>
<td>2192</td>
<td>963.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>NN distance x Tree height x Cluster membership</td>
<td>2</td>
<td>2379</td>
<td>1190</td>
<td>522.8</td>
<td>&lt;0.001</td>
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<tr>
<td>Residuals</td>
<td>22525</td>
<td>513415</td>
<td>2</td>
<td></td>
<td></td>
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</tbody>
</table>
**Figure 1.** Tree locations at Ash Meadows National Wildlife Refuge derived from object-based classification of LiDAR and multispectral data.
Figure 2. Example of the (a, d) true-color multispectral image, (b, e) soil-adjusted vegetation index (SAVI), and (c, f) combined normalized digital surface model (nDSM; red channel) and slope of the nDSM (green channel) without (a-c) and with (d-e) an overlay of delineated trees. In the SAVI images (b,e), the red color indicates vegetation.
In the combined nDSM and slope of nDSM images (c, f), green to red indicates height and the slope of the nDSM defines the lighter green border of each tree.

**Figure 3.** Examples delineation error in the object-based classification of individual trees due to adjacency of trees in woodlands. The red outline shows the delineation of a single tree object, while the (a) normalized digital surface model (nDSM), (b) slope of the nDSM, and (c) soil-adjusted vegetation index (SAVI) images suggest there should be two trees, as identified in the field.
Figure 4. The relationship between the local pair correlation function \((g(r))\) across distances \(r = 0\) to \(40\ m\) and height of the focal tree. Local \(g(r) = 1\) signifies random association, with values \(< 1\) indicating regularity and values \(> 1\) indicating clumping.
Figure 5. The relationship between the local pair correlation function \((g(r))\) across distances \(r = 0\) to \(40\) m and distance to surface water. Local \(g(r) = 1\) signifies random association, with values < 1 indicating regularity and values > 1 indicating clumping.
Figure 6. The relationship between mean height and distance of the four nearest neighbors (NN) for trees located in clusters of (a) small and (b) large trees.
APPENDIX A. SUPPLEMENTARY MATERIAL FOR CHAPTER 2.

Figure 1. Mean (±SE) final number of leaves for tree seedlings under salinity and depth to water treatments.
Table 1. Pearson’s correlation coefficients between soil variables measured in the field experiment, including gravimetric soil water content (GSWC), bulk density, volumetric soil water content (VSWC), porosity, air-filled porosity, degree of saturation, pH, and electrical conductivity (EC).

<table>
<thead>
<tr>
<th></th>
<th>GSWC</th>
<th>Bulk density</th>
<th>VSWC</th>
<th>Porosity</th>
<th>Air-filled porosity</th>
<th>Degree of saturation</th>
<th>pH</th>
<th>EC</th>
</tr>
</thead>
<tbody>
<tr>
<td>GSWC</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bulk density</td>
<td>-0.28</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>VSWC</td>
<td>0.81</td>
<td>0.15</td>
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<td></td>
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<tr>
<td>Porosity</td>
<td>0.59</td>
<td>-0.31</td>
<td>0.35</td>
<td>1</td>
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<tr>
<td>Air-filled porosity</td>
<td>-0.52</td>
<td>-0.36</td>
<td>-0.77</td>
<td>0.18</td>
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<td></td>
<td></td>
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<tr>
<td>Degree of saturation</td>
<td>0.75</td>
<td>0.22</td>
<td>0.90</td>
<td>0.25</td>
<td>-0.88</td>
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<tr>
<td>pH</td>
<td>-0.27</td>
<td>0.07</td>
<td>-0.21</td>
<td>-0.16</td>
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**Table 2.** Parameter estimates, 95% confidence intervals, and p-values from 10,000 MCMC simulations for linear mixed models of soil variables as a function of location (transect and standardized distance along transect) and sampling time (measurement month and year).

<table>
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<th>Soil variable</th>
<th>Estimate</th>
<th>2.5% CF</th>
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<th>p</th>
<th>Transect</th>
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<th>B</th>
<th>C</th>
<th>D</th>
<th>Distance</th>
<th>Month</th>
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<td>-0.190</td>
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Table 2 continued.

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Figure 1. Relative risk of seedling emergence of Prosopis glandulosa associated with vegetation treatments, the volumetric soil water content (VSWC) and electrical conductivity (EC) stress gradients, and plant cover.
Figure 2. Relative risk of seedling emergence of *Prosopis pubescens* associated with vegetation treatments, the volumetric soil water content (VSWC) and electrical conductivity (EC) stress gradients, and plant cover.
Figure 3. Relative risk of seedling emergence of *Fraxinus velutina* associated with vegetation treatments, the volumetric soil water content (VSWC) and electrical conductivity (EC) stress gradients, and plant cover.
Figure 4. Relative risk of death of emergent *Prosopis glandulosa* seedlings associated with vegetation treatments, the volumetric soil water content (VSWC) and electrical conductivity (EC) stress gradients, and plant cover.
Figure 5. Relative risk of death of emergent *Prosopis pubescens* seedlings associated with the volumetric soil water content (VSWC) and electrical conductivity (EC) stress gradients and plant cover. There were no interactions with vegetation treatment included in the averaged model.
Figure 6. Relative risk of death of emergent *Fraxinus velutina* seedlings associated with vegetation treatments, the volumetric soil water content (VSWC) and electrical conductivity (EC) stress gradients, and plant cover.
Figure 7. Relative risk of death of planted seedlings of *Prosopis glandulosa* and *Fraxinus velutina* associated with the volumetric soil water content (VSWC) and electrical conductivity (EC) stress gradients and plant cover.