THESIS

Factors affecting seedling recruitment of the desert shrub *Atriplex polycarpa* (Torr.) S. Watson (Chenopodiaceae) in the San Joaquin Valley of California

Mitchell L. Coleman, B.S.

A Thesis Submitted to the Department of Biology
California State University, Bakersfield
In Partial Fulfillment for the Degree of Masters of Science

Fall 2017

Fall 2017

Factors affecting seedling recruitment of the desert shrub *Atriplex polycarpa* (Torr.) S. Watson (Chenopodiaceae) in the San Joaquin Valley of California

Mitchell L. Coleman

This thesis has been accepted on behalf of the Department of Biology by their supervisory committee:

Dr. R. Brandon Pratt
Committee Chair

Dr. Anna L. Jacobsen
Committee Member

David J. Germano

Dr. David J. Germano
Committee Member

Dr. Michael D. White
Committee Member

Table of Contents

Page

Acknowledgements

I am tremendously grateful for the mentorship of my graduate advisor, Dr. Brandon Pratt, who has provided keen intellect, insight, training, and esprit de corps throughout the past two years in all aspects of my research and the writing of my thesis. I also thank the other members of my thesis committee: Drs. David Germano, Anna Jacobsen, and Michael White, for their substantive comments, advice, and guidance which have greatly improved the quality of my research. I also thank the substantial input, advice, and support of Dr. Ellery Mayence of the Tejon Ranch Conservancy. Thanks also go to various departments and offices at California State University, Bakersfield: the Biology Department, the Office of Grants, Research, and Sponsored Programs (GRaSP), the Office of University Advancement, the School of Natural Sciences, Mathematics, and Engineering (NSME), and the President's Associates, for providing and administering sources of funding which have enabled me to carry out this endeavor: the Student Research Scholars (SRS) program and the Environmental Educational Partnership Impacting Colleges and Careers (EPIC). I also thank the National Science Foundation (NSF) Center for Research Excellence in Science and Technology (CREST) grant (HRD-1547784) for funding my research. Thanks also go to the Tejon Ranch Conservancy and Mrs. Gayle Batey for the unique opportunities they provided to conduct my research at Tejon Ranch. By extent, I thank the Tejon Ranch Company for providing access to their property. Thanks also go to Dr. Adam Guo, Elizabeth Powers, and Morgan Kayser of the CSUB Geology Department for helping me run the soil analyses. In addition, I would like to thank my fellow graduate student Marta Percolla for her valuable feedback and assistance with the making of figures. Thanks also go to Alex Baer, Emily van Ryn, Eva Arrieta, and Logan Salazar for helping me with data collection in the field and for twice helping me dig my truck out when stuck in streams. I thank my employer, Quad Knopf Inc., for allotting me the time needed to complete my thesis work. I also thank my friends Stephen Avila, Daniel Malouf, and Dave Constance for their support and encouragement. Lastly, I thank my wife Lindsey, my son Harry, my parents Donna and Lewis Coleman, and my in-laws Michael, Sherry, Robert, and Ellen Whitehead, for their steadfast patience, emotional support, logistical support, and love. This project was far from a solo effort and I am very grateful for all the support from the many individuals and organizations listed above. Thank you, all.

Abstract

Invasive annual grasses of mediterranean origin dominate large areas in the arid and semi-arid regions of the San Joaquin Valley in California and create numerous management challenges. Much of the invaded habitat would be native saltbush shrub communities (*Atriplex* spp.); however, the presence of these grasses may inhibit saltbush recruitment. One way this could occur is due to competition for water between the grasses and saltbush seedlings. Another possibility is that when invasive annual grasses die after setting seed, they leave behind a dense cover of residual dry matter (RDM) as dead shoots, which alters the habitat by shading the soil. I tested the hypothesis that grasses limit saltbush seedling recruitment, leading to persistently invaded grasslands and thereby inhibiting saltbush succession. I predicted that competition from grasses during the rainy season reduces soil moisture available to saltbush seedlings at the critical seedling stage of their life cycle. Furthermore, I predicted that the presence of dense RDM blankets formed during the dry season shades the soil and inhibits the natural succession of saltbush shrublands in the San Joaquin Valley at old-field areas. Moreover, I predicted that grass competition and RDM affects saltbush recruitment due to alterations in soil temperature, soil moisture, and light penetration to the ground.

To address these questions, I used a combination of manipulative and natural field experiments to assess the factors affecting recruitment of the saltbush *Atriplex polycarpa* (Torr.) S. Watson. I conducted experiments manipulating the effects of invasive grass competition and RDM on saltbush seedling germination, mortality, and survival. I also conducted a number of comparative studies between six mature saltbush stands at Tejon Ranch, wherein I assessed differences in seedling recruitment, demographic composition, water relations, and soil conditions. The goal of the study was to more precisely elucidate mechanisms governing saltbush germination in the San Joaquin Valley.

Overall, I found than invasive grass RDM functions to inhibit saltbush seed germination to a degree that precludes long-term seedling recruitment in the San Joaquin Valley. Competition between saltbush seedlings and the grasses during the wet season also inhibits recruitment to a smaller degree. Saltbush recruitment is affected by alterations to soil moisture, temperature, and light levels created by invasive grasses. I also found that older seedling survival is greater in grassy areas compared to native saltbush habitat, ostensibly due to higher pressures of herbivory in the saltbush habitat. This creates a seed-seedling conflict wherein seed

germination is inhibited in grassy areas, but seedling survival is higher in grassy areas. Thus, field conditions with a low amount of RDM over saltbush seeds and no seedling herbivory are ideal for saltbush recruitment in the San Joaquin Valley. My findings are relevant for the conservation and management of important remaining saltbush habitat and the continued expansion of invasive annual grasses in the San Joaquin Valley and throughout the mediterranean-type climate regions of California.

List of Tables

CHAPTER 2

CHAPTER 3

List of Figures

CHAPTER 2

CHAPTER 3

Chapter 1

Background and Purpose of the Study

Invasive species

Human beings have transformed the earth at various scales since their evolution, which has ushered in the current geologic age known as the Anthropocene. The last 150 y have seen over a sevenfold increase in human population, up to 7.3 billion in 2011, from under 1 billion prior to 1850, increasing the demand for resources from earth's natural systems (Holdren and Ehrlich 1974, Primack 2011). Technological advancements during this time have dramatically increased the capacity of humans for transforming and manipulating these systems. These factors have made the spread of human civilization a global ecological force with consequences for the earth's climate and biodiversity. One of the challenges is to ensure that the earth's systems do not get degraded to the point where they are no longer able to provide the vital services of clean air, water, and other raw materials upon which human well-being depends. A related challenge is to stem the unprecedented rate of species extinctions that are taking place in what has been called the earth's sixth mass extinction event (Millennium Ecosystem Assessment 2005, Barnosky et al. 2011).

An important contributing factor to biodiversity loss, second only to habitat loss, is related to the movement of some species outside of their natural ranges by human activities, either intentionally or by accident (National Research Council 1995). Anthropogenic modes of transportation have allowed humans to transport species all over the earth. When a species arrives in a new location, the vast majority of new arrivals perish, while a minority may survive and become established. Even fewer of these species that establish ever spread to cause harm, and it is these species that are called invasive (Wilson 2009, Pysek and Richardson 2010). The annual cost of coping with invasive species and their effects on the environment is estimated to be over $335 billion worldwide, and over $120 billion in the United States alone (Pimentel et al. 2005, Whitney and Gabler 2008). Approximately 400 of the 1300 species under the Endangered Species Act listed as either threatened or endangered were listed primarily because of predation, competition, disease, habitat alteration, hybridization, or other pressures imposed by invasive species (Pimentel et al. 2005, USFWS 2012).

Because of the importance of invasive species in biodiversity and economic loss, biotic invasions have been the focus of intensive study for the last three decades (Blossey and Kamil 1996, Vitousek et al.1997, Gordon 1998, Hamilton et al. 1999, Callaway and Aschehoug 2000, Lambrinos 2000, Kolar and Lodge 2001, Sakai et al. 2001, Keeley 2002, Hellmann et al. 2008, Mackinnon et al. 2014). Many studies suggest that there may be a common set of factors that explain why some species become invasive. A high priority goal has been to identify these key factors to gain predictive power that can be used to inform policies and practices aimed at preventing future invasions. Moreover, understanding the factors of why some species become invasive and the effects of invasive species on native systems is essential for developing effective management, mitigation, and restoration strategies.

There are often multiple reasons for why a species becomes invasive. One factor is that invasive species commonly have a suite of traits that contribute to their invasive nature. For example, tolerance of disturbance, high fecundity, phenotypic plasticity, and rapid growth and maturation characterize many invasive species (Baker 1974, Baker 1991, Blossey and Kamil 1996, Vitousek et al. 1997, Gordon 1998, Callaway and Aschehoug 2000). Another important factor is the enemy release hypothesis, which posits that invasive species spread rapidly in distribution and abundance due to a lack of specialist predators and pathogens present in their native ranges, which allows them to allocate resources to growth and reproduction instead of to defense, in turn making them more competitive (Keane and Crawley 2002, Liu and Stiling 2006, Gooden et al. 2009). In some cases, invaders may be more resistant to abiotic stress (Funk et al. 2008), but this may be rare (MacKinnon et al. 2014; Pratt and Black 2006).

There are also factors that affect the invasibility of a particular region. For example, plant invasions are commonly facilitated by natural or anthropogenic landscape disturbances that lead to gaps in native vegetation cover (Corbin and D’Antonio 2004). This creates recruitment opportunities to establish in areas that would otherwise remain resistant to invasion. On the other hand, biodiverse communities may be more resistant to invasion in what is called the Biotic Resistance Hypothesis (Elton 1958, Levine et al. 2004). Also, habitats characterized by low resources (i.e., low soil nitrogen availability) are often considered to be more resistant to invasions; conversely, those that are characterized by high levels of resources may be more easily invaded. Although there are some generalities that pertain to many invaders, a unified theory of biotic invasions is lacking and may not be attainable due to the multiple pathways open to invaders. This does not mean that every invasion is idiosyncratic, and efforts aimed at generalizations and identification of common invasive pathways remains as an important research priority towards predicting future invasions.

Annual grass invasions in the southwestern United States

In the lower to mid-elevations of the arid and semi-arid western United States, invasive annual grasses are among the most widespread and problematic of all invasive plants. These invasive grasses do especially well in habitats disturbed by humans, but of most concern, they can also invade into minimally disturbed natural areas (Corbin and D'Antonio 2004). During the widespread settlement of Europeans in the last 200 y, much of the western United States was intentionally sown with annual grasses originating from the Mediterranean Basin to support cattle grazing, ranching, and agricultural operations, in addition to unintentional dispersion of stowaway species in feed and fur (Baker 1978, Mack 1978). The genera of grasses that are among the most important in this invasion include *Avena* (oat), *Bromus* (brome grass), *Hordeum* (barley), *Schismus* (mediterranean grass), and *Vulpia* (fescue) (Jackson 1985, Germano et al. 2001).

The invasive grasses have numerous negative effects in these regions. In some cases, the grasses grow in such dense stands that they crowd out native plant species and decrease species richness (Yelenik and Levine 2011). These grasses germinate early in the growing season and produce fibrous and shallow roots (Wainwright et al. 2012). Roots of the grasses commonly share the same root space in the soil as co-occurring native perennial seedlings and annuals, which can have a strong effect on native plant survival through direct competition for water and nutrients (Yelenik and Levine 2011). The residual dry matter (RDM) formed from the senesced shoots of the grasses does not rapidly decompose after the growing season due to limited water availability that restricts biotic decomposition. The RDM can occur in dense blankets that shade and cool the soil, which can inhibit some native seedlings from germinating and establishing (Bartolome 1979, Eliason and Allen 1997, Bartolome et al. 2007). Decomposition at this time is primarily through photodegradation and this leads to about an 8-10% reduction in mass, with the remaining mass persisting through the summer (Eviner 2016). The decreased soil temperature can also increase soil moisture available to the established deeper-rooted perennial natives, increasing productivity (Wood et al. 2006). The RDM can be thick and impenetrable making it difficult for some small vertebrate species (some federally listed as threatened or endangered) to move on the landscape, increasing incidence of predation, and decreasing survival (Germano et al. 2011).

One of the most important effects that some of these invasions have is to alter the fire regime in many of these areas in what has been called the grass-fire cycle. The presence of these invasive grasses in these regions disrupts the regular fire regime by changing the fuel properties, altering fire behavior (intensity, spread, and seasonality), leading to more frequent fire return intervals, and can lead to fires in systems where fire would otherwise not be present. In deserts, which lack adequate fuel to carry a fire, the invasion of grass may introduce a fuel matrix that can carry a fire. This is particularly detrimental in such systems because the native species are not adapted to fire and fail to regenerate after such a disturbance (Germano et al. 2012; Fig. 1). In such cases it may take decades for the native perennial vegetation to recolonize the site and if the cycle of fire continues then the perennials will never reestablish (Brooks et al. 2004).

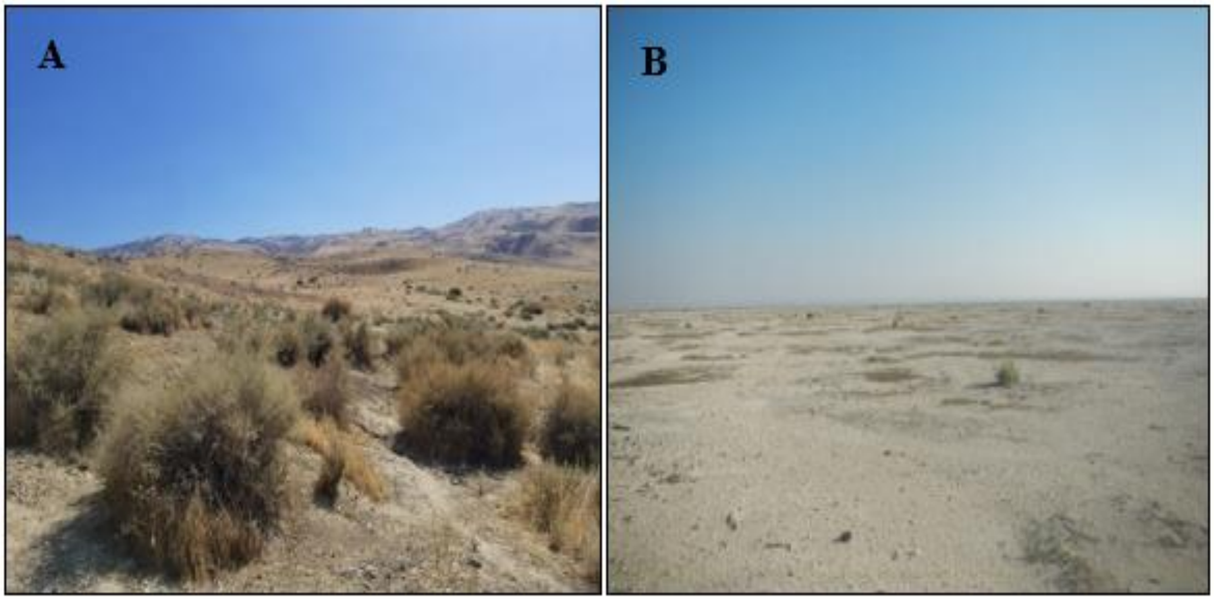

Figure 1. A) an unburned mature saltbush (*Atriplex polycarpa*) stand in the foreground in October 2016, minimally invaded by annual grasses, in the San Joaquin Valley of California, B) a saltbush site in June 2016 burned by accidental wildfire in May 1997 that was facilitated by the residual dry matter of invasive annual grasses, verified as a prior saltbush stand by personal communication with D. Germano of California State University, Bakersfield. In the 19 years since the fire, there has been minimal succession of saltbush and the site now consists mostly of invasive grasses and bare ground maintained by small vertebrates (Photographs by M. Coleman).

The San Joaquin Valley of California

The San Joaquin Valley (SJV) in the southern two-thirds of the Central Valley of California constitutes one of the single greatest anthropogenic landscape alterations in history and has become one of the world's most productive agricultural regions (USGS 1993). During the initial influx of Europeans to the SJV in the early 19th Century, large areas of land were cleared for ranching, agriculture, and later, petroleum and industrial operations, along with steady urban development. Prior to this development, the valley floor and surrounding foothills harbored a mosaic of plant communities comprised of perennial bunch grasslands, oak woodlands, saltbush shrublands, riparian woodlands, freshwater marshes, and vernal pools. These habitats supported large numbers of rodents, birds, reptiles, large predators, and other wildlife, many endemics to the region, forming complex food webs and supporting indigenous peoples (Faber 1997, Germano et al. 2011). This system was highly productive benefitting from warm temperatures, abundant sunshine, and nutrient-rich alluvial soils.

The climate in this area is a Mediterranean-type, with hot, dry summers, and cool, moist winters with highly variable annual rainfall on the valley floor (Lambrinos 2000, Keeley 2002, Germano et al. 2011). The southern and western portions of the SJV are a desert due to the low levels of annual rainfall (about 150 mm/year average from 1985-2005; Faber 1997) and similarity in biotic composition and structure to other North American deserts, such as the Mojave Desert to the east (Germano et al. 2011). The climatic similarity and the human disturbance regime that has been common in the Mediterranean Basin are both important reasons why the southern SJV has come to be dominated by annual grasses of Mediterranean origin (Jackson 1985, Hamilton et al. 1999, Germano et al. 2001, Corbin and D'Antonio 2004). Droughts may have also been a contributing factor in the establishment and expansion of the Mediterranean grasses (Corbin and D'Antonio 2004). The combination of anthropogenic development and disturbance and the expansion of the invasive grasses were chief factors leading to the reduction and fragmentation of populations or extinction of many once-common plant and animal species (Faber 1997, Germano et al. 2001, 2012).

Valley Saltbush Shrublands

An extensive vegetation type in the SJV is the Valley Saltbush Shrubland (VSS) community (Fig. 1A). This community is an open-structured shrubland dominated by perennial shrubs in the family Chenopodiaceae that are commonly called saltbushes. Four common chenopods in VSS are *Atriplex polycarpa* (Torr.) S. Watson (valley saltbush), *A. spinifera* J. F. Macbr. (spiny saltbush), *A. canescens* (Pursh) Nutt. (four-wing saltbush), and *A. lentiformis* (Torr.) S. Watson (quailbush). Depending on how wet a site is in winter and the salinity and alkalinity of the soil, other species may be present such as *Suaeda nigra* J.F. Macbr. (bush seepweed), *Frankenia salina* (Molina) I. M. Johnston (alkali heath), *Allenrolfea occidentalis* (S. Watson) Kuntze (iodine bush), and *Isocoma acradenia* E. Greene (goldenbush). Valley saltbush shrublands commonly occur in upland and moderately saline habitats in the southern and southwestern portions of the valley and on the Carrizo Plain, along alluvial fans, washes, and hills of the valley floor, mostly on sandy soils with low surface alkalinity. Commonly interspersed between the shrubs are native and alien annual forbs (e.g. *Amsinckia* spp.), as well as abundant invasive annual grasses in the genera *Hordeum*, *Bromus*, *Avena*, and *Shismus*.

Today VSS largely exists as remnant fragmented stands of a once much larger range (Holland 1986, Philips et al. 2015). The community has been largely extirpated from the valley floor due to cattle operations, urban developments, fire, and agriculture production. Remnant stands of VSS occur, of which less than 5% remains, commonly in areas that cannot be effectively farmed due to saline soils or other factors (Fig. 2; Sankary and Barbour 1972, Holland 1986, Faber 1997). The relatively open VSS is preferred habitat for many animal species, some of which are federally listed as threatened or endangered (e.g., San Joaquin Kit Fox, *Vulpes macrotis mutica*, Giant Kangaroo Rat, *Dipodomys ingens*, Tipton Kangaroo Rat, *D. nitratoides nitratoides*, Blunt-Nosed Leopard Lizard, *Gambelia sila*). By contrast, sites heavily invaded by grasses form dense blankets of RDM (Fig. 3C) in years when the rainfall quantity and timing is conducive to grasses. In such years the abundant RDM limits the mobility of these animals, leaving them more susceptible to predation and unable to forage as effectively (Germano et al. 2011).

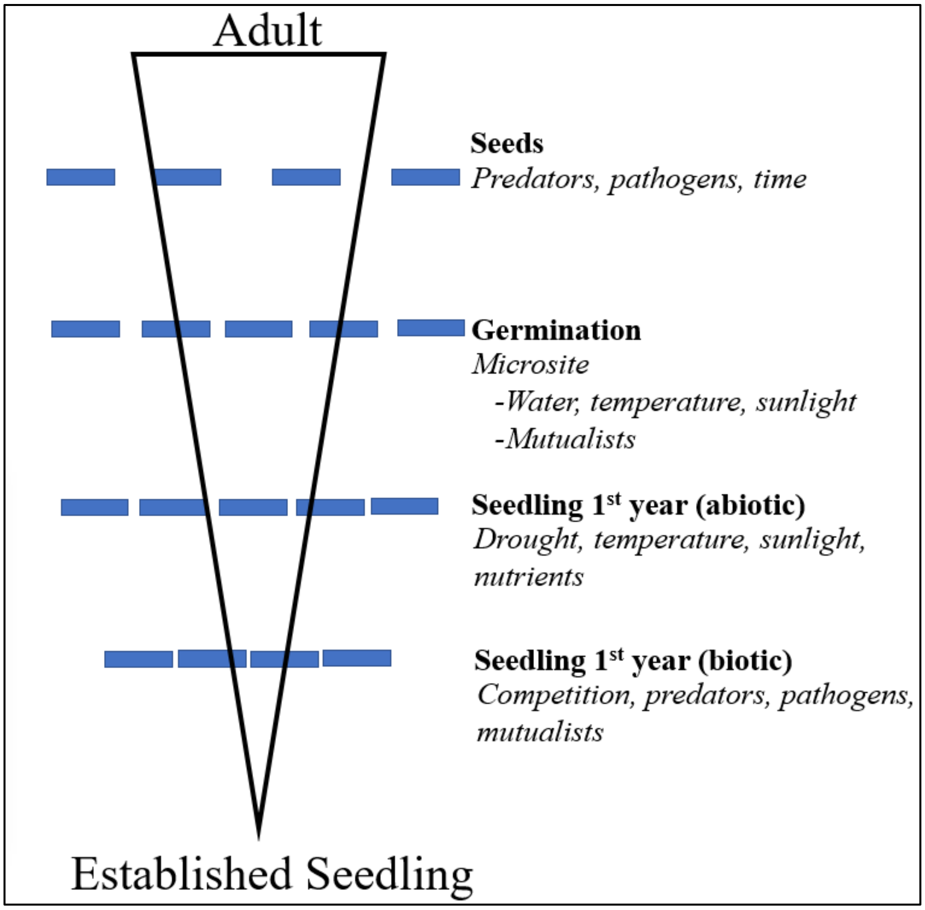

Figure 2. Filter model of the factors affecting seedling recruitment of saltbush shrubs (*Atriplex polycarpa*) in the San Joaquin Valley of California. Large mature shrubs produce an abundance of viable seeds during the growing season (September-January) but relatively few seeds germinate in most years. Seeds that do germinate (February-March) undergo significant mortality in the first year. The combination of significant seed production, minimal germination, and minimal seedling survival means that the capacity of mature saltbush shrubs to produce established seedlings is very low (elements of an r-selected species).

Atriplex polycarpa, a common dominant shrub of VSS sites, is an important plant in this ecosystem. The shrub forms vital forage and cover for native wildlife and cattle, and is the only significant source of browse available when annual plants are dormant during the dry season. Consequently, the shrub has often been heavily browsed by cattle as it satisfies all nutritional requirements (Chatterton et al. 1971, Sankary and Barbour 1972), leading to one common name of cattle spinach. Species in the genus *Atriplex* are known to provide effective erosion control and stabilization of disturbed soils (Mikhiel et al. 1992), preventing dust from blowing into the atmosphere, especially during years of drought. Non-native grasslands in developed areas do not provide this same service (Corbin and D’Antonio 2004). As the SJV has some of the poorest air quality in the United States (Chow et al. 1993), much of which is a result of dry dust from disturbed sites, established stands of VSS help to protect the air quality of this region. *Atriplex* shrubs may be useful in conservation and management, and revegetation efforts have been successful (Mikhiel et al. 1992); however, there is a need to understand the specific seedling establishment characteristics of saltbush as an aid to guide restoration and management efforts.

Saltbush, invasive grasses, and residual dry matter

As land use has changed over time, it is common to find previously used lands from oil, industry, range, and agricultural purposes become abandoned and left fallow. Due to their disturbed nature, these areas often become colonized and dominated by widely dispersed invasive grasses and forbs. Some of these invaded sites exist as a patchwork interspersed in areas where native VSS communities remain. It appears in some cases that these invaded areas are relatively stable, and that native VSS vegetation is not colonizing the apparently suitable habitat, potentially preventing the succession of these sites to a mature VSS community. It is even possible that in some cases these invaded old-field areas may represent a stable and alternative community-type (De Steven 1991, Beisner et al. 2003). At the very least, the invasive species are likely slowing natural successional processes. One way this could happen is due to the dense RDM formed by these invasive grasses and forbs (Fig. 3C), a unique structural modification that is not present to the same degree in the remnant patches of native vegetation. The RDM can produce dense blankets capable of 100% ground cover, reaching up to 50 cm in height, and persisting for multiple years (Corbin and D’Antonio 2004). In contrast, VSS is an open community with relatively little ground cover (Fig. 1A).

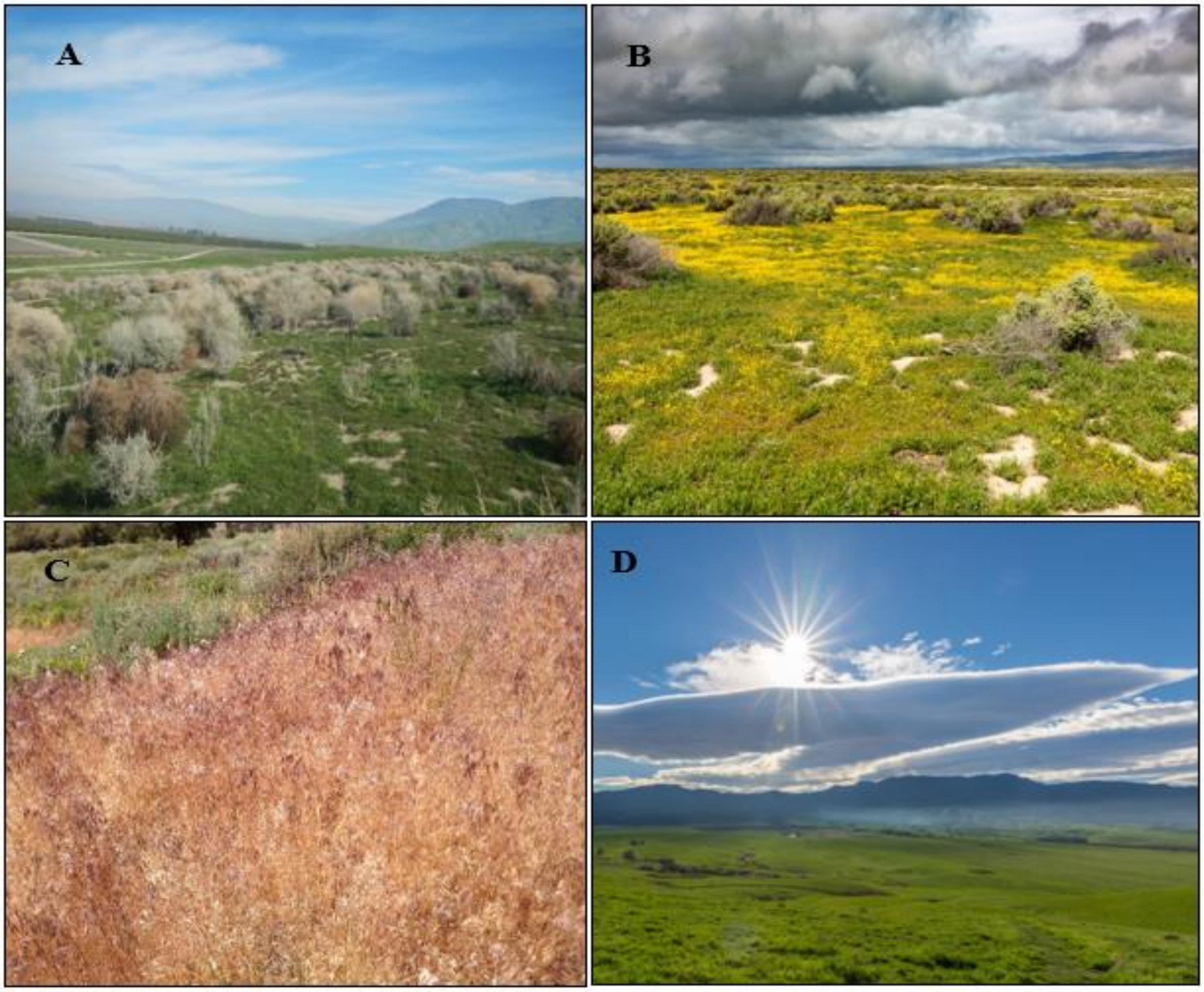

Figure 3. A) A small stand of Valley Saltbush Scrub (VSS) with an understory of annual grasses, located on Tejon Ranch in the western foothills of the Tehachapi Mountain Range. B) A stand of VSS with an understory composed of Golden Fields (*Lasthenia californica*), Filaree (*Erodium cicutarium*), and Tidy Tips (*Layia platyglossa)* in bloom at the north end of the Carrizo Plain. C) Non-native annual grassland and abundant residual dry matter following flowering in southern San Joaquin Valley near the foothills of the Tehachapi Mountain Range. D) Non-native annual grassland at Tejon Ranch in the southern San Joaquin Valley in the foothills of the Tehachapi Mountain Range during the rainy season of 2016 (Photographs by M. Coleman [A & C] and R. B. Pratt [B & D]).

The combination of grasses (Fig. 3D) and their RDM (Fig. 3C) may modify air and soil temperature, soil moisture, and light penetration to the soil to a degree that inhibits germination of *A. polycarpa* seeds, or prevents seedlings from establishing. Germination of *Atriplex* species and other arid desert shrubs are affected by variations in temperature, light, and water availability (Sankary and Barbour 1972, Khan and Ungar 1984, Mikhiel et al. 1992, Khan and Rizvi 1994, Khan and Ungar 1997, Glenn and Brown 1998, Dodd and Donovan 1999, Bajji et al. 2002, Mandak 2003, Khan et al. 2004, Jacobsen et al. 2009), thus there is reason to believe that the annual grasses and their RDM could alter seed germination. Germination in *A. polycarpa* is reduced by strong light exposure and increased by high water availability, and is has a temperature optimum of 9-15°C (Sankary and Barbour 1972). In this context, RDM may promote germination, but it may lead to lower survival of seedlings that germinate in the shade of the RDM. Annual grasses are rare in the native SJV flora and RDM may not have reached such high levels in pre-invasion native VSS stands.

One reason why RDM may exert such a strong negative effect on *A. polycarpa* seedlings is related to its photosynthetic physiology. *Atriplex polycarpa* has a C4 photosynthetic pathway while the grass and forb competitors have C3 photosynthesis. There are some invasive forbs that germinate and grow late in the spring and summer that are C4 photosynthetic (e.g. Russian thistle; *Salsola* spp.), but their populations are generally much less abundant and associated with very high disturbance habitats. The type of photosynthetic pathway is important because C3 plants are more quantum efficient than C4 plants; it takes at least two additional ATP to fix a CO_2 molecule for a C4 plant than a C3 plant (Skillman 2008). This ATP comes from the light reactions in photosynthesis, thus in high-light conditions the extra ATP is not a prohibitive cost and the advantages of the C4 pathway become manifest. The chief advantages are that C4 plants have negligible photorespiration and this increases their carbon fixation efficiency compared to C3 plants. This advantage allows them to fix CO_2 at very low concentrations in their leaves, thus allowing them to leave their stomata less open or open to the same degree for less amount of time while achieving the same amount of CO_2 fixation as co-occurring C3 plants (Ehleringer and Pearcy 1983, Oberhuber et al. 1993). The outcome of this is that water use efficiency (mass of CO_2 fixed per quantity of water lost) of C4 plants is generally higher than C3 plants (Ehleringer and Bjorkman 1977).

Because C3 plants have higher quantum efficiency, they perform better under low light conditions than C4 plants. Under the cover of dense RDM, the shaded conditions may put C4 *A. polycarpa* seedlings at a competitive disadvantage against the C3 grasses and forbs. Moreover, C3 plants have higher rates of photorespiration at higher temperatures, which lowers their photosynthetic rates while C4 plants are unaffected by temperature (Ehleringer and Bjorkman 1977). In summary, under dense RDM, temperature conditions may be cooler and that coupled with shade will produce an environment that favors C3 photosynthesis over C4. This advantage may lead to greater competitive success of C3 grasses and forbs at the early seedling stage beneath the RDM.

Saltbushes do not appear to readily expand and recruit into grass-dominated landscapes, which is the primary observation that is motivating this study. My observations in the field suggest that strong light exposure and low water availability during drought may create an opening in grass dominated habitats that allow the saltbush to germinate without competition from invasive grasses and their RDM. I tested the hypothesis that grasses limit saltbush seedling recruitment, leading to persistently invaded grasslands and thereby inhibiting saltbush succession. I predicted that competition from grasses during the rainy season reduces soil moisture available to saltbush seedlings at the critical seedling stage of their life cycle. I predicted that the presence of dense RDM formed during the dry season shades the soil and inhibits the natural succession of VSS in the SJV at old-field areas. Moreover, I predicted that RDM affects saltbush germination and survival due to alterations in soil temperature, soil moisture, and light penetration to the ground.

Literature Cited

Bajji, M., J. M. Kinett, and S. Lutts. 2002. Osmotic and ionic effects on NaCl on germination, early seedling growth, and ion content of *Atriplex halimus* (Chenopodiaceae). Canadian Journal of Botany 80:297-304.

Baker, H. G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics 1:1-24.

Baker, H. G. 1991. The continuing evolution of weeds. Economic Botany 45:445-449.

Barnosky, A D., N. Matzke, S. Tomiya, G. O. Wogan, B. Schartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, KC Maquire, B. Mersey, and E. A. Ferre. 2011. Has earth’s sixth mass extinction already arrived? Nature 471:51-57.

Bartolome, J. W. 1979. Germination and seedling establishment in California annual grassland. Journal of Ecology 67:273-281.

Bartolome, J. W., R. D. Jackson, A. D. K. Betts, J. M. Connor, G. A. Nader, and K. W. Tate. 2007. Effects of residual dry matter on net primary production and plant functional groups in Californian annual grasslands. Grass and Forage Science 62:445-452.

Beisner, B. E., D.T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1:376-382.

Blossey, B., and J. Kamil. 1996. What determines the increased competitive ability of invasive non-indigenous plants? Proceedings of the IX international symposium on biological control of weeds: pp. 3-9. Stellenbosch, South Africa.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. Ditomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. Bioscience 54:677-688.

Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:521-523.

Chatterton, N. J., J. R. Goodin, C. M. Mckell, R. V. Parker, and J. M. Rible. 1971. Monthly variation in the chemical composition of desert saltbush. Journal of Range Management 24:37-40.

Chow, J. C., J. G. Watson, D. H. Lowenthal, P. A. Solomon, K. L. Magliano, S. D. Ziman, and L. W. Richards. 1993. PM10 and PM2.5 compositions in California's San Joaquin Valley, Aerosol Science and Technology, 18:2, 105-128.

Cleland, E. E., J. L. Funk, and E. B. Allen. 2016. Coastal Sage Scrub. Pages 429-448 in Ecosystems of California. Mooney, H., and E. Zavaleta, editors. University of California, Press. Berkeley, California.

Corbin, J. D., and C. M. D'Antonio, 2004. Competition between native perennial and exotic annual grasses: implications for a historical invasion. Ecology 85:1273-1283.

Daubenmire, R. F. 1959. Plants and environment: a textbook of plant autecology. John Wiley and Sons Inc., New York, New York.

De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology 72:1076-1088.

Dix, R. L. 1961. An application of the point-centered quarter method to the sampling of grassland vegetation. Journal of Range Management 14:63-69.

Dodd, G. L., and L. A. Donovan. 1999. Water potential and ionic effects on germination and seedling growth of two cold desert shrubs. American Journal of Botany 86:1146-1153.

Eliason, S. A. and E. B. Allen. 1997. Exotic grass competition in suppressing native shrubland re-establishment. Restoration Ecology 5:245-255.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, UK.

Ehleringer, J. R., and O. Bjorkman 1977. Quantum yields for CO_2 uptake in C_3 and C_4 plants. Plant Physiology 59:86-90.

Ehleringer, J. R., and R. W. Pearcy.1983. Variation in quantum yield for CO_2 uptake among C_3 and C_4 plants. Plant Physiology 73:555-559.

Eviner, V. T. 2016. Grasslands. Pages 449-477 in Ecosystems of California. Mooney, H., and E. Zavaleta, editors. University of California Press. Berkeley, California.

Faber, P. 1997. California's Wild Gardens: A Guide to Favorite Botanical Sites. University of California Press. Berkeley, California.

Fenn, M. E., J. S. Baron, E. B. Allen, H. M. Rueth, K. R. Nydick, L. Geiser, W. D. Bowman, J. O. Sickman, T. Meixner, D. W. Johsnon, and P. Neitlich. 2003. Effects of nitrogen deposition in the western United States. Bioscience 53:404-420.

Floyd, D. A., and J. E. Anderson. 1987. A comparison of three methods for estimating plant cover. Journal of Ecology 75:221-228.

Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution 23:695-703.

Germano, D. J., G. B. Rathburn, and L. R. Saslaw. 2001. Managing exotic grasses and conserving declining species. Wildlife Society Bulletin 29:551-559.

Germano, D. J., G. B. Rathburn, L. R. Saslaw, B. L. Cypher, E. A. Cypher, and L. M. Vrendenburgh. 2011. The San Joaquin Desert of California: ecologically misunderstood and overlooked. Natural Areas Journal 31:138-147.

Germano, D. J., G. B. Rathburn, and L. R. Saslaw. 2012. Effects of grazing and invasive grasses on desert vertebrates in California. The Journal of Wildlife Management 76:670-682.

Glenn, E. and J. Brown. 1998. Effects of soil salt levels on the growth and water use efficiency of *Atriplex canescens* (Chenopodiaceae) varieties in drying soil. American Journal of Botany 85:10-16.

Gooden, B., K. French, P.J. Turner, and P.O. Downey. 2009. Impact threshold for an alien plant invader, *Lantana camara* L., on native plant communities. Biological Conservation 142:2631-2641.

Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecological Concepts in Conservation Biology 8(4):975-989.

Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. Oecologia 121:518-526.

Heady, H. F., T. C. Foin, M. K. Hektner, D. W. Taylor, M. G. Barbour, and W. J. Barry. 1988. Valley grassland. Pages 491-514 in M. G. Barbour and J. Major, editors. Terrestrial Vegetation of California, 2nd ed. California Native Plant Society, Sacramento, California.

Hellmann, J. J., J. E. Byers, and B. G. Bierwagen, and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. Conservation Biology 22:534-543.

Holdren, J. P., and P. R. Ehrlich. 1974. Human population and the global environment: population growth, rising per capita material consumption, and disruptive technologies have made civilization a global ecological force. American Scientist 62:282-292.

Holland, R. F. 1986. Preliminary description of the terrestrial natural communities in California. Natural Diversity Database, California Department of Fish and Game, Sacramento, California.

Jackson, L. E. 1985. Ecological origins of California's Mediterranean grasses. Journal of Biogeography 12:349-361.

Jacobsen, A. L., R. B. Pratt, L. M. Moe, and F. W. Ewers. 2009. Plant community water use and invisibility of semi-arid shrublands by woody species in southern California. Madroño 56:213-220.

Keane, R. M. and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17:164-170.

Keeley, J. E. 2002. Fire and invasive species in Mediterranean-climate ecosystems in California. U.S. Geological Survey, Los Angeles, California. Accessed online at http://www.globalrestorationnetwork.org/uploads/files/LiteratureAttachments/144_fire-and-invasive-species-in-mediterranean-climate-ecosystems-of-california.pdf

Khan, M. A., and We. A. Ungar. 1984. The effects of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex triangularis* Willd. American Journal of Botany 71:481-489.

Khan, M. A., and We. A. Ungar. 1996. Influence of salinity and temperature on the germination of *Haloxylon recurvum* Bunge ex Boiss. Annals of Botany 78:547-551.

Khan, M. A., and We. A. Ungar. 1997. Effects of light, salinity, and thermoperiod on the seed germination of halophytes. Canadian Journal of Botany 75:835-841.

Khan, M., and Y. Rizvi. 1994. Effect of salinity, temperature, and growth regulators on the germination and early seedling growth of *Atriplex griffithi* var. *stocksii*. Canadian Journal of Botany 72:475-479.

Khan, M., B. Gul, and D. J. Weber. 2004. Temperature and high salinity effects in germinating dimorphic seeds of *Atriplex rosea*. Western North American Naturalist 64:193-201

Kings County Association of Governments (KCAG). 2011. Regional Transportation Plan and Sustainable Communities Strategy. Final Program Environmental Impact Report. Kings County Association of Governments, Fresno, California.

Kolar, C. S. and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16:199-204.

Lambrinos, J. G. 2000. The impact of the invasive alien grass *Cortaderia jubata* (Lemoine) Stapf on an endangered Mediterranean-type shrubland in California. Diversity and Distributions 6:217-231.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1-18.

Levine, J. M., P. B. Alder, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7:975-989.

Liu, H., and P. Stiling.2006. Testing the enemy release hypothesis: a review and meta-analysis. Biological Invasions 8:1535-1545.

MacKinnon, E. D., R. B. Pratt, A. L. Jacobsen. 2014. Functional trait differences between weedy and non-weedy plants in southern California. Madroño 61:328-338.

Malmstrom, C. M., A. J. McCullough, H. A. Johnson. L. A. Newton, and E. T. Borer. 2005. Invasive annual grasses indirectly increase virus incidence in California native perennial bunchgrass. Oecologia 145:153-164.

Mandak, B. 2003. Germination requirements of invasive and non-invasive *Atriplex* species:a comparative study. Flora 198:45-54.

Mikhiel, G. S., S. E. Meyer, and R. L. Pendleton. 1992. Variation in germination response to temperature and salinity in shrubby *Atriplex* species. Journal of Arid Environments 22:39-49.

Millennium Ecosystem Assessment (MEA). 2005. Ecosystems and human well-being. 4 volumes. Island Press, Covelo, California.

National Research Council. 1995. Science and the endangered species act. National Academy of Science, Washington D.C., USA.

Oberhuber, W., Dai, Z., and Edwards, G. E. 1993. Light dependence of quantum yields in photosystem II and CO2 fixation in C3 and C4 plants. Photosynthesis Research 35:265-274.

Philips, S., P. Kelly, and D. Williams. California State University, Stanislaus. 2015. Landscape change in the San Joaquin Valley of California; natural communities. Endangered Species Recovery Program, Fresno, California. Accessed online at https://databasin.org/datasets/9d98c56b03104a4386cc8858ebfea031.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273-288.

Pratt, R. B., and R. A. Black. 2006. Do invasive trees have an advantage over native trees? Biological Invasions 8:1331-1341.

Primack, R. B. 2012. A Primer of Conservation Biology. 5th ed. Sinauer Associates, Inc. Sunderland, Massachusetts.

Pysek, P., and D. M. Richardson. 2010. Invasive Species, environmental change and management, and health. Annual Review of Environmental Resources 35:25-55.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, We. M. Paker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology 32:305-320.

Sankary, M. N., and M. G. Barbour. 1972. Autecology of *Atriplex polycarpa* from California. Ecology 53:1155-1162.

Skillman, J. B. 2008. Quantum yield variation across the three pathways of photosynthesis: not yet out of the dark. Journal of Experimental Botany 59:1647-1661.

United States Fish & Wildlife Service (USFWS). 2012. The Cost of Invasive Species. United States Fish & Wildlife Service. http://www.fws.gov.

United States Geological Survey (USGS). 1993. San Joaquin Valley, California. United States Geological Survey. http://pubs.usgs.gov/circ/circ1182/pdf/06SanJoaquinValley.pdf

Venable, D. L., and L. Lawlor. 1980. Delayed germination and dispersal in desert annuals: escape in space and time. Oecologia 46:272-282.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. New Zealand Journal Ecology. 21:1-16.

Wainwright, C. E., E. M. Wolkovich, and E. E. Cleland. 2012. Seasonal priority effects: implications for invasion and restoration in a semi-arid system. Journal of Applied Ecology 49:234-241.

Whitney, K. D, and C. A. Gabler. 2008. Rapid evolution in introduced species, 'invasive traits' and recipient communities :challenges for predicting invasive potential. Diversity and Distributions 14:569-580.

Wilson, J. R., E. E. Dormontt, P. J. Prentis, and A. J. Lowe. 2009. Something in the way you move: dispersal pathways affect invasion success. Trends in Ecology and Evolution 24:136-144.

Wood, Y. A., T. Meixner, P. J. Shouse, and E. B. Allen. 2006. Altered ecohydrologic response drives native shrub loss under conditions of elevated nitrogen deposition. Journal of Environmental Quality 35:76-92.

Yelenik, S. G., and J. M. Levine. 2011. The role of plant-soil feedbacks in driving native-species recovery. Ecology 92:66-74.

Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution 16:454-459.

Chapter 2

The effects of invasive grass on seedling recruitment of native *Atriplex polycarpa* (Torr.) S. Watson (Chenopodiaceae) shrubs in the San Joaquin Valley of California

Mitchell L. Coleman and R. Brandon Pratt

Department of Biology, California State University, Bakersfield, 9001 Stockdale Hwy,
Bakersfield CA, 93311

Abstract

In the San Joaquin Valley of California, invasive annual grasses have widely invaded upland habitats of native saltbush communities. We tested the hypothesis that grasses limit saltbush seedling recruitment, leading to persistently invaded grasslands and thereby inhibiting saltbush succession. We predicted that this could happen due to competition for water between grasses and saltbush seedlings. Alternatively, a dense cover of residual dry matter (RDM) produced by the grasses may negatively impact saltbush seeds by affecting soil temperature and light-demanding seedlings by shading them. We conducted an experiment manipulating grass competition, RDM presence, and shade (shade cloth control with no RDM) over a two-year period. We measured, on a seasonal basis, seedling emergence (germination), mortality rate, survival, and growth (% vegetative coverage) for the saltbush *Atriplex polycarpa*. We also monitored soil moisture and temperature across the treatments and surface soil temperature. Grass competition and RDM both reduced *A. polycarpa* germination and survival, though RDM had a larger treatment effect than competition. Seedling survival was low in all treatments, but the rate of survival was lower in the competition and RDM treatments. Coverage of *A. polycarpa* was reduced by RDM, but not by competition. Soil moisture and temperature at 10 cm depth did not vary with RDM or competition treatments, although both varied by season. Surface soil temperatures were decreased by the presence of shade. We conclude that invasive grasses negatively influence the recruitment of *A. polycarpa* in the San Joaquin Valley, and that the primary mechanism through which this occurs is through inhibition of saltbush germination by a dense cover of RDM. Land management strategies aimed at reducing RDM should benefit saltbush seedling recruitment.

*Key Wor*ds: residual dry matter, competition, Valley Saltbush Shrublands.

Introduction

In the lower elevations of the arid and semi-arid southwestern United States, annual grasses of Mediterranean origin are among the most widespread and invasive of non-indigenous plants. These invasive grasses perform especially well in habitats disturbed by humans, and some of the most invasive can colonize minimally disturbed natural areas (Corbin and D’Antonio 2004). The genera of grasses that are among the most important in this invasion include *Avena* spp. (oat), *Bromus* spp. (brome grass), *Hordeum* spp. (barley), and *Festuca* spp. (fescue) (Jackson 1985). These grasses are almost exclusively native to the Mediterranean Basin and have invaded climatically similar areas in California (Corbin and D’Antonio 2004).

Mediterranean invasive grasses have long posed numerous management challenges throughout California. Areas that are heavily invaded by grasses often have significantly reduced species richness compared to similar habitats that have not been invaded (Yelenik and Levine 2011; Wainwright et al. 2012). In some cases, the grasses grow in such dense stands that they crowd out native plant species entirely, creating large monotypic grasslands (Yelenik and Levine 2011). The grasses often germinate early in the growing season and quickly produce fibrous and shallow roots, enabling them to effectively compete for space, light, and nutrients. This can be a significant competitive advantage over later germinating natives (Wainwright et al. 2012, Mackinnon et al. 2014).

The residual dry matter (RDM) formed from the senesced shoots of the grasses in the dry season does not rapidly decompose due to limited water availability restricting biotic decomposition (Corbin and D’Antonio 2004; Eviner 2016). The RDM represents a unique structural modification that is not present to the same degree in native vegetation, wherein communities tend to be more open with relatively little ground cover aside from low-growing annual forbs in the spring. Dense RDM can shade the soil, reducing the light level at the soil surface and potentially reducing soil temperature. This combination can inhibit some native seedlings from germinating and establishing, especially light-loving species that thrive in open canopy and warm soil conditions (Bartolome 1979, Bartolome et al. 2002, Eliason and Allen 1997, Bartolome et al. 2007). Shade produced by RDM could be especially detrimental to seedlings of plants with a C_4-type photosynthetic pathway, such as saltbushes (*Atriplex* spp.), which are adapted to sunny and warm conditions and have a lower quantum efficiency than C_3 plants (Ehleringer and Pearcy 1984).

Atriplex spp. are known to thrive in saline, alkaline, and are moderately tolerant of disturbance, thus they may be beneficial for habitat restoration in the arid southwestern region of the United States (Ciblis et al. 1998). Some revegetation efforts have been successful (Chatterton et al. 1971, Mikhiel et al. 1992); however, there are gaps in understanding the factors controlling seedling recruitment that hamper efficient restoration and management efforts in the region. In saltbush shrublands in the San Joaquin Valley (SJV) of California, invasive annual grasses and forbs are common among mature saltbush shrubs, and are abundant in areas adjacent to stands of shrubs. These invaded areas appear to be relatively stable and the adjacent saltbush vegetation is not colonizing apparently suitable habitat, potentially preventing the succession of these sites to a more extensive saltbush community. These invaded areas may represent an alternative stable community to saltbush shrubland (De Steven 1991, Beisner et al. 2003). At the very least, the invasive grasses are likely slowing successional processes that would otherwise lead to a native community of VSS.

A common native vegetation type in the southern SJV is the Valley Saltbush Shrub (VSS) community. This community occurs across arid upland and moderately saline habitats across the southern SJV and on the Carrizo Plain, along alluvial fans, washes, and hills of the valley floor, mostly on sandy soils with low surface alkalinity (Sankary and Barbour 1972). This community is an open shrubland dominated by shrubs in the family Chenopodiaceae. Two of the most common chenopods in VSS are valley saltbush, *Atriplex polycarpa* (Torr.) S. Watson, and spiny saltbush, *A. spinifera* J.F. Macbr. Saline lowland sites may also contain Bush Seepweed (*Suaeda nigra* J.F. Macbr), Alkali Heath (*Frankenia grandifolia,* We. M. Johnston), Iodine Bush (*Allenrolfea occidentalis* S. Watson), and Goldenbush (*Isocoma acradenia* var. *bracteosa* E. Greene) (Holland 1986). These shrublands were once common at upland sites across the valley floor, but have been reduced to less than 5% of the original range (Faber 1997). The California Department of Fish and Wildlife now considers VSS to be a sensitive natural community and conservation is a priority (California Natural Diversity Database 2017).

We worked with *A. polycarpa* because it is a common dominant and representative shrub species of the VSS community in the southern SJV. We hypothesized that dense stands of invasive annual grasses inhibit saltbush shrubland succession. We predicted that resource competition from the grasses during the rainy season would reduce soil moisture available to saltbush seeds and seedlings at a critical stage their life cycle, thereby inhibiting germination, increasing mortality, and decreasing survival. The formation of dense RDM during the dry season shades the soil, limiting the light level at the soil surface and lowering soil temperature. Because of this, we predicted that RDM would inhibit saltbush seedling recruitment. Moreover, we predicted that the combination of invasive grass competition and RDM would lower saltbush recruitment due to alterations in soil temperature, soil moisture, and light penetration to the ground.

Methods

We tested *A. polycarpa* seedling recruitment by manipulating invasive grass competition and RDM across a series of experimental plot treatments in a former cotton field that is now an ecological preserve (Environmental Studies Area or ESA) on campus at California State University, Bakersfield, in a former floodplain of the Kern River. The preserve has a sandy soil composition and is dominated by invasive mediterranean grass and forb species including *Hordeum vulgare* L., *Bromus madritensis* L. ssp. *rubens* (L.) Hunshot, *Bromus diandrus* Roth, and *Erodium cicutarium* (L.) L'H-r., as well as a weedy native forb, *Amsinckia menziesii* (Lehm.) Nelson & J.F. Macbr, thus providing suitable conditions to test our hypothesis. Additionally, *A. polycarpa* shrubs had been transplanted on the site in the last 10 y and have since recruited seedlings in controlled bare patches adjacent to the planted shrubs (pers. obs.). Thus, the site provides suitable conditions for saltbush, and naturally occurring stands of saltbush can be found < 1 km away.

We established ninety 2 × 5 dm plots on 5 December 2015, prior to the onset of winter rains and freezing temperatures. We randomized plot placement and orientation within the study area, which was approximately 100 x 100 m of flat area in the ESA with uniform environmental conditions and dominated by invasive annual grasses. We completely cleared each plot of vegetation by raking away the RDM of the previous year and by hand weeding where necessary. The plots were marked and anchored with numbered pin flags or rebar (depending on the treatment, see below) at each corner to ensure the same area was surveyed over the course of the study. We then sowed seeds of *A. polycarpa* in the plots (100 seeds per plot) and we randomly spread them with a rake. We manipulated invasive grass competition and RDM with the following treatments: 1) RDM was either directly added to a specified amount (see below) or not added (+/- RDM); 2) plots were either weeded or unweeded to test competition (+/- weeded); and 3) shade cloth was pegged about 0.5 m over plots to specifically control for the shade generated by RDM (+Shade Cloth). We randomly assigned each plot to one of six treatments (n = 15 plots/ treatment): 1) +RDM/ -Weeded, 2) -RDM/ -Weeded, 3) +RDM/ +Weeded, 4) -RDM/+Weeded, 5) +Shade Cloth/-Weeded, and 6) +Shade Cloth/ +Weeded.

We standardized the amount of RDM added to +RDM plots by adding RDM until the light level at the soil surface underneath the RDM was approximately 300 µmols of quanta m^{-2} s^{-1} measured on a clear sunny day at solar noon (ambient light level at solar noon ~ 2000 µmols quanta m^{-2} s^{-1}; Li 250A, Li-Cor Corporation, Lincoln, Nebraska, USA). This light level corresponded to the amount of shade produced from the moderately dense RDM (approximately 0.0015 kg dry mass/m^2). The RDM that was added to plots came from the site. It consisted primarily of shoots of *H. vulgare* and *B. diandrus*. When weeding, care was taken to avoid disturbing *A. polycarpa* seeds and seedlings in the plots. This was best accomplished by frequent visits to the site when the grasses and forbs were just germinating (January-March) so they could be removed when recently germinated and very small. We weeded plots concurrently with the repeated plot measurements.

For the shade cloth treatments, we fastened commercial shade cloth (model # 72015, Easy Gardener Inc., Waco, Texas, USA) with binder clips to rebar at a height of 0.5 m over the plots. We draped the shade cloth around the rebar to inhibit light to the soil surface, while also allowing for air flow over the soil. We standardized the degree of light inhibition at the soil surface in the shade cloth plots (i.e., the number of layers of shade cloth) to correspond with the light inhibition level of the +RDM plots (300 µmols quanta m^{-2} s^{-1}). In this case, one layer of shade cloth was sufficient to inhibit the light level at the soil surface to approximately 300 µmols quanta m^{-2} s^{-1}. This treatment was designed to specifically recreate only the shade cast by the RDM because the C4 saltbushes might be particularly sensitive to shade.

To determine effects of the treatments, we measured *A. polycarpa* vegetative coverage (percentage of plant growth covering each plot) and density (individuals/ plot) from 16 February 2016 (right after germination) to 26 January 2017. We used a 2 × 5 dm quadrat that was color coded to aid in rapid collection of coverage and density data (Daubenmire 1959). We standardized collection of data for vegetative coverage to avoid bias by visually assigning coverage of each plot into one of six coverage classes: 1 (0–5%), 2 (5–25%), 3 (25–50%), 4 (50–75%), 5 (75–95%), 6 (95–100%). We determined coverage by analyzing the total percentage of ground covered by *A. polycarpa* within each plot, then assigning each species the appropriate coverage class. We measured density by counting all the individuals per plot.

We installed soil moisture and temperature probes at a 10-cm depth (n = 3 per treatment) to measure soil moisture (m^2 soil/m^2 H_2O) and temperature (°C) between treatments (Decagon 5TM, ECTM, and EC20 soil probes; Decagon Devices, Pullman, Washington, USA). We installed the probes underneath the plots and did not disturb the plot soil. We chose to measure at 10 cm because this is a root depth at which we predicted *A. polycarpa* seedlings and invasive grasses would share soil space and compete for resources. Data from the soil probes were mostly collected concurrently with the other measurements. We monitored the amount rainfall at the site with a standard manual rain gauge (Stratus Precision Rain Gauge with Mounting Bracket, 14’’ All Weather, San Diego, California). We also continuously measured ambient air temperature every two hours throughout the experiment with air temperature data loggers suspended at 0.5m (Pendant HOBO temperature data logger; Onset, Cape Cod, Massachusetts, USA). One shielded temperature logger was left in the open to monitor air temperature in the sun, and a second was suspended inside a shade cloth treatment to monitor air temperature in the shade. Lastly, we measured soil surface temperatures between open-air and shade cloth treatments with an IR thermometer on 29 September 2017 to assess differences (Fluke 572 Infrared Thermometer, Fluke Corporation, Everett, Washington, USA).

We made measurements approximately every other week after initial germination in the winter and spring of 2016 to capture the rapid germination and mortality that occurred during that time (February-April). We thereafter continued to take measurements at least once a month depending on how rapidly germination, growth, and mortality of *A. polycarpa* was occurring. During the summer months, most annual species had senesced so weeding and measurements were less frequent at that time. For consistency, we recorded each temperature and moisture measurement period between 1100 and 1200.

Statistical Analyses

We tested for differences in *A. polycarpa* density, *A. polycarpa* vegetative coverage, soil moisture, and soil temperature using ANOVA or Kruskal-Wallis models (a non-parametric equivalent). Independent variables in all models included two treatment factors that both had two levels (+RDM and –RDM; +Weeded and –Weeded). We included a shade cloth treatment that simulated the shade of the +RDM in some plots and was only replicated across the +weeded and –weeded treatments. Initial analyses included plot as a treatment factor and time was included as a random repeated measures treatment factor; however, this model was not able to test key aspects of our experiment, so time was removed by separately analyzing different points in time (see details below). We checked data for normality and equal variances and we transformed data if these assumptions were not met. We used non-parametric statistical models when transformations failed. We used methods described by Barnard et al. (2007) and implemented in Microsoft Excel (Microsoft Corporation, Bellingham, Washington, USA) and Minitab 18^{TM} software (Minitab Inc., State College, Pennsylvania, USA) to analyze data, and Type I error rate was set at 0.05. We used pre-planned independent contrasts to test for differences between individual factor levels (+RDM vs. -RDM, +RDM vs. +Shade cloth, and +weeded vs. -weeded plots).

We separately analyzed the density of *A. polycarpa* (# of individuals/ plot) at three distinct time periods to capture key aspects of the response to the treatments that included the peak density within each plot, which represented the amount of germination of the original 100 seeds added to each plot (Kruskal-Wallis test). A second analysis was the time to 50% mortality (time in days to density at 50% reduction from peak density within each plot) that estimated mortality rate. This analysis was done by calculating the slope of the relationship between seedling density plotted over time for each plot and treatment. We omitted plots fewer than three points (i.e., with little or no germination) from the regression. We $\log_{10}$ transformed data to satisfy the assumptions of ANOVA. The last factor we measured was the number of seedlings alive at the end of the experiment on a per plot basis, which gave the final measurement of survival.

We compared survival of seedlings across the treatments to field plots of naturally occurring saltbush stands for context of how naturally occurring seedlings survive. To do this, we analyzed the total number of surviving *A. polycarpa* individuals by treatment (from 26

January 2017, the last measuring period) with a chi-square goodness of fit test. The total number of surviving individuals was used as the observed value for each treatment level. For the expected value we used the stand density of naturally occurring saltbush stands in the SJV. We measured the density (all shrubs within a 30-m radius) of six mature VSS stands in the SJV located at Tejon Ranch approximately 30 km south of our study area. The native VSS stands contained an average 0.081 shrubs/m^2 (Coleman, unpubl. data). This corresponded to an expected value of 0.202 shrubs for the amount of area we sampled at our field site (15 plots x 0.1 m^2/plot). We further analyzed the survival data by individual factor levels to assess pairwise interactions (+RDM vs. -RDM, +RDM vs. +Shade cloth, and +weeded vs. -weeded plots) using chi-square tests with the Yate's correction (observed = sum of survivors for each factor level, expected = 0.202 shrubs in native VSS).

We used a modified Kruskal-Wallis test to account for repeated measures to assess significance in *A. polycarpa* coverage (the data were non-normal). We analyzed coverage differences across all six treatments: between 1) +RDM/ -Weeded, 2) -RDM/ -Weeded, 3) +RDM/ +Weeded, 4) -RDM/+Weeded, 5) +Shade Cloth/-Weeded, and 6) +Shade Cloth/ +Weeded. We also used independent *a priori* contrasts to test for pairwise differences between individual factor levels (+RDM vs. -RDM, +RDM vs. +Shade cloth, and +weeded vs. -weeded plots). Methods were followed in Barnard et al. (2007).

We separately analyzed variation in soil moisture and soil temperature (at 10 cm depth) by treatment (n = 6, see above) and by season (n = 5, winter 2016 to winter 2017) with Kruskal-Wallis tests. This was done to relate treatment and seasonal variation in soil conditions to the predicted effects on *A. polycarpa* germination (Winter 2016), and mortality (Spring to Fall 2016) and survival (Winter 2017) of seedlings. To avoid pseudoreplication, the mean was taken for each season. To account for individual sensor differences, we analyzed the soil moisture data as percentages of the maximum for each sensor. We also analyzed soil surface temperature variation between full sun plots (n = 60) and shade cloth plots (n = 30) with a one-way ANOVA.

Results

The total amount of onsite rainfall during the 2015–2016 rainfall season (June 2015-June 2016) was 97.5 mm, which is below the yearly average in the region of 163.83 mm. In contrast, the total rainfall for the 2016–2017 rainfall was slightly more than the regional average at 173.37 mm (Fig. 1). Soil moisture at 10 cm depth varied by season ($H = 104.77$, df = 4, $P < 0.001$) as would be predicted in a mediterranean-type climate region. Soil moisture was generally lower in the summer and fall and higher in the winter and spring (Table 1). Soil moisture also varied by treatment ($H = 51.43$, df = 5, $P < 0.001$). The presence of RDM did not affect soil moisture compared to the absence of RDM, whereas the +RDM treatment had reduced soil moisture relative to the +shade cloth plots. Weeded and unweeded plots did not differ in soil moisture (Fig. 1, Table 1).

Soil temperature at 10 cm depth did not vary by treatment ($H = 1.79$, df = 5, $P < 0.877$), though it did vary by season ($H = 163.75$, df = 4, $P < 0.001$). Soil temperature at 10 cm was higher in Summer 2016 compared to both Winter 2016 and Spring 2016. Summer 2016 temperature was greater than Fall 2016, and Fall 2016 soil temperature was greater than Winter 2017 (Fig. 2). Throughout the measuring period, air temperature was warmer in the full sun compared to inside the shade cloth treatment, except in early January 2016 (Fig. 3). Also, midday soil surface temperature was greater in open-air plots (-RDM and +RDM) compared to the +shade cloth plots ($F_{1,59} = 562.86$, $P < 0.001$).

Seedlings germinated *en masse* between 20 and 24 February 2016. The maximum number of seeds that germinated varied among the treatments ($H = 37.74$, df = 5, $P < 0.001$; Fig. 4A). The +RDM plots had significantly lower germination of seedlings when compared to the -RDM treatment (Fig. 4B). The shade cloth covered plots did not reduce germination to the degree of +RDM plots (Fig. 4C), suggesting that RDM affected germination in ways other than simply casting shade. Competition for resources from the invasive grasses also impacted germination, though not to the same degree as RDM (Fig. 4D, Tables 2 and 3).

Overall, mortality rate was greatest among the +RDM treatments ($F_{1,5} = 8.29$, $P < 0.001$; Fig. 5A, Table 2), whereas competition with the grasses did not influence saltbush mortality rate (Table 4). The total number of surviving seedlings varied among the treatments ($\chi^2 = 877.2$, df = 5, $P < 0.050$) (Fig. 5A, Table 2). Seedlings in +RDM plots had lower survival compared to seedlings in -RDM plots ($\chi^2 = 551.14$, df = 1, $P < 0.001$; Fig. 4B). Seedlings in +RDM had greater mortality than the shading treatment, indicating that the RDM affected survival by more than simply shading the soil ($\chi^2 = 367.02$, df = 1, $P < 0.001$; Fig. 4C). Seedlings in -weeded plots had lower survival compared to seedlings in +weeded plots ($\chi^2 = 2040.1$, df = 1, $P < 0.001$; Fig. 4D).

Vegetative cover varied between the treatments ($H = 107.86$, df = 5, $P < 0.001$). The presence of RDM significantly reduced coverage compared to the absence of RDM. Similarly, +RDM plots significantly reduced coverage compared to the shade cloth group. Lastly, +weeded plots did not affect coverage of saltbush compared to -weeded plots (Tables 2 and 5).

Discussion

Residual dry matter from invasive grasses had a large effect on saltbush recruitment in our experiments. The biggest effect in the experiment was the reduction in seed germination in the +RDM plots. The reproductive life history traits of *A. polycarpa* seems to be characteristic of an r-selected species because they produce abundant seed and seedlings with high mortality rates during the first year. With this reproductive pattern, factors that limit germination greatly reduce successful recruitment of seedlings because most of the seedlings suffer mortality in this arid and highly seasonal environment. This result supports our hypothesis that the presence of invasive grasses likely limits saltbush succession in areas where there are remnant stands of saltbush; moreover, our manipulative study pinpoints the presence of invasive grass RDM as the most important mechanism limiting the expansion of saltbush stand into otherwise suitable habitat.

The effect of RDM on saltbush germination could be due to a range of factors and one that we specifically considered in this study was shading. Shading of the soil offers a partial explanation for the effect of RDM on saltbush germination and survival. We predicted the shade effect was important because *A. polycarpa* is a C4-photosynthetic species, thus it has higher photosynthetic light requirements (lower quantum efficiency) than a typical C3 photosynthetic plant (Ehleringer and Pearcy 1983). The shade cloth treatment reduced light levels at the soil surface and surface air temperatures that probably had an important effect on germination. Seeds appear to be both light and temperature sensitive and have a narrow optimum for maximum germination. Saltbush germination in the lab is has been shown to occur optimally at soil temperatures between 9–15 °C and is inhibited at temperatures lower and higher than the optimal range (Sankary and Barbour 1972). Outdoor soil temperatures at 10 cm depth were within this range at the time of germination; however, the soil surface temperature was likely different than soil temperature in experiencing a broader range of temperatures because they were not insulated by the soil. Surface soil temperature would likely have been closer to air temperature than 10 cm deep in the soil. Air temperatures were significantly warmer in the full sun compared to underneath the shade cloth at the time of germination, and this was likely an important factor in altering germination.

One way the shade cloth treatment differs from RDM is that the RDM lies directly on the soil surface of the plots, while the shade cloth was raised off the soil. This difference could have something to do with the different response between the shade plots and the +RDM plots. Dense RDM could exert a mechanical effect when it is laying directly on seedlings; however, our plots were not that dense and there were gaps in the RDM that seedlings could easily grow through to avoid mechanical strain. The shade cloth also helped to retain soil moisture to a degree that RDM did not.

There are additional factors that we did not directly test that could be related to the effect of RDM on saltbush germination and survival. For example, the RDM may provide a substrate for microorganisms that significantly alter the microbiota (Hawkes et al. 2005, Batten et al. 2006). The well-studied grass pathogen *Puccinia graminis* (stem rust disease) is known to produce survival structures, called teliospores, on the shoots of infected grass hosts when they senesce, which are then capable of infecting non-grass species (Leonard and Szabo 2005). The link between RDM and microbiota is an area for future study.

While RDM had the largest effect on saltbush germination, competition from grasses also led to reduced overall germination and survival compared to plots with no competition. In this water-limited environment, we predicted that grasses would compete with saltbush seedlings for soil resources. Our measurements of soil moisture at 10 cm depth did not support this prediction because soil moisture did not vary between weeded (no competition) and unweeded (competition) plots. It may be that competition for resources largely occurs at soil depths shallower than 10 cm. Competition also played a role in the shade cloth treatment as there was greater germination and survival in the +shade/+weeded treatment compared to +shade/-weeded one. The C3 grasses would have had a competitive advantage in the shade due to the previously mentioned lower quantum efficiency of C4-photosynthetic *A. polycarpa*.

Our results predict that an environment that is low in grass cover should be best for saltbushes. From 2012–2015, California experienced drought conditions (Diffenbaugh et al. 2015). During 2014–2016, especially in 2016, we observed abundant *A. polycarpa* seedling recruitment at many stands throughout the SJV, including at the site in the present study. Presumably, the years of little precipitation led to reduced grass production and RDM and had allowed saltbush germination and survival. Low levels of RDM were observed at that time (pers. obs.). The rainfall in 2017 was about average and, as of March 2017, few saltbush seeds germinated in the SJV, whereas many seedlings were evident at the same time in 2016. These observations could be tested with field plots that manipulate rainfall (rain out shelters). This an important consideration from a land management perspective, because it would mean that controlling for RDM during the dry season, instead of controlling for competition during the wet season (as is often done), would be a more effective method for increasing saltbush germination rates.

VSS provides valuable ecological services to the San Joaquin Valley. For example, saltbushes provide effective erosion control and stabilization of soils (Mikhiel et al. 1992), mitigating particulate matter from blowing into the atmosphere, especially during years of drought to a degree that annual grasslands do not. VSS also provides important habitat for a few special-status species that are endemic to the valley, including the Giant Kangaroo Rat (*Dipodomys ingens*), Blunt-nosed Leopard Lizard (*Gambelia sila*), and the San Joaquin Kit Fox (*Vulpes macrotis mutica*) (Germano et al. 2001). Management efforts such as cattle grazing, mowing, and herbicide treatments that reduce the competitive edge of invasive annual grasses, and by extent their capacity to produce RDM, may aid in VSS restoration efforts geared at converting alternately stable invasive grasslands to mature saltbush shrublands.

In summary, we found that invasive annual grasses diminish *A. polycarpa* germination, increase the rate of mortality, decrease vegetative growth, and decrease survival of seedlings at an early critical stage of development. In the first year of life, saltbush seeds in heavily invaded sites germinate in lower numbers, experience greater mortality, and produce fewer established seedlings. Specifically, it seems that presence of RDM along with direct competition, is the main factor limiting saltbush recruitment in the SJV.

Acknowledgements

We thank Anna Jacobsen and David Germano of CSU Bakersfield, as well as Mike White of the Tejon Ranch Conservancy, for their comments on the manuscript. We also thank the Student Research Scholars (SRS) program at CSU Bakersfield for providing funds that enabled us to carry out this project. Lastly, we thank Emily van Ryn for assisting with data collection.

Literature Cited

Baker, H. G. 1978. Invasion and replacement in California and neotropical grasslands. Commonwealth Scientific and Industrial Research Organization, Melbourne, Victoria, Australia.

Baker, J. B., R. J. Southard, and J. P. Mitchell. 2005. Agricultural dust production and standard conservation tillage systems in the San Joaquin Valley. Journal of Environmental Quality 34:1260-1269.

Bajji, M., J. M. Kinett, and S. Lutts. 2002. Osmotic and ionic effects on NaCl on germination, early seedling growth, and ion content of *Atriplex halimus* (Chenopodiaceae). Canadian Journal of Botany 80:297-304.

Barnard, C., G. Francis, and P. McGregor. 007. Significance tests. Pp. 91-100 in Asking Questions in Biology. Pearson Education Limited, Essex, UK.

Bartolome, J. W. 1979. Germination and seedling establishment in California annual grassland. Journal of Ecology 67:273-281.

Bartolome, J. W., Frost, W. E., McDougland, N. K., and M. Connor. 2002. California guidelines for residual dry matter (RDM) management on coastal and foothill annual rangelands. Agriculture and Natural Resources Publication 8092:1-7.

Bartolome, J. W., R. D. Jackson, A. D. K. Betts, J. M. Connor, G. A. Nader, and K. W. Tate. 2007. Effects of residual dry matter on net primary production and plant functional groups in Californian annual grasslands. Grass and Forage Science 62:445-452.

Batten, K. M., K. M. Scow, K. F. Davies, and S. P. Harrison. 2006. Two invasive plants alter soil microbial community composition in serpentine grassland. Biological Invasions 8:217-230.

Beisner, B. E., D.T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1:376-382.

Brown, J., K. Benedict, B. J. Park, and G. R. Thompson. 2013. *Coccidioidomycosis*: epidemiology. Clinical Epidemiology 5:185-197.

California Department of Fish and Wildlife (CDFW). 2017. California Natural Diversity Database, Rarefind Version 3.1.0. Accessed online at https://www.wildlife.ca.gov/Data/CNDDB.

Chatterton, N. J., J. R. Goodin, C. M. Mckell, R. V. Parker, and J. M. Rible. 1971. Monthly variation in the chemical composition of desert saltbush. Journal of Range Management 24:37-40.

Chow, J. C., J. G. Watson, D. H. Lowenthal, P. A. Solomon, K. L. Magliano, S. D. Ziman, and L. W. Richards. 1993. PM10 and PM2.5 compositions in California's San Joaquin Valley, Aerosol Science and Technology, 18:2, 105-128.

Ciblis, A. F., Swift, D. M., and E. D. McArthur. 1998. Plant-herbivore interactions of *Atriplex*: current state of knowledge. Gen. Tech. Rep. RMRS-GTR-14. Ogden, Utah. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Cleland, E. E., J. L. Funk, and E. B. Allen. 2016. Coastal Sage Scrub. Pages 429-448 in Ecosystems of California. Mooney, H., and E. Zavaleta, editors. University of California Press, Berkeley, California.

Corbin, J. D., and C. M. D'Antonio, 2004. Competition between native perennial and exotic annual grasses: implications for a historical invasion. Ecology 85:1273-1283.

Daubenmire, R. F. 1959. Plants and environment: a textbook of plant autecology. John Wiley and Sons Inc., New York, New York.

De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology 72:1076-1088.

Diffenbaugh, N. S., D. L. Swain, and D. Touma. 2015. Anthropogenic warming has increased drought risk in California. Proceedings of the National Academy of Sciences 112:3931-3936.

Dodd, G. L., and L. A. Donovan. 1999. Water potential and ionic effects on germination and seedling growth of two cold desert shrubs. American Journal of Botany 86:1146-1153.

Egerton-Warburton, L.M. and Allen, E.B., 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. Ecological applications 10:484-496.

Eliason, S. A. and E. B. Allen. 1997. Exotic grass competition in suppressing native shrubland re-establishment. Restoration Ecology 5:245-255.

Ehleringer, J. and R. W. Pearcy. 1983. Variation in quantum yield for CO_2 uptake among C3 and C4 plants. Plant Physiology 73:555-559.

Eviner, V. T. 2016. Grasslands. Pp. 449-477 in Ecosystems of California. Mooney, H., and E. Zavaleta, editors. University of California Press, Berkeley, California.

Faber, P. 1997. California's Wild Gardens: A Guide to Favorite Botanical Sites. University of California Press, Berkeley, California.

Fenn, M.E., Baron, J. S., Allen, E. B., Rueth, H. M., Nydick, K. R., Geiser, L., Bowman, W. D., Sickman, J. O., Meixner, T., Johnson, D.W. and P. Neitlich, 2003. Ecological effects of nitrogen deposition in the western United States. BioScience 53:404-420.

Germano, D. J., G. B. Rathburn, and L. R. Saslaw. 2001. Managing exotic grasses and conserving declining species. Wildlife Society Bulletin 29:551-559.

Germano, D. J., G. B. Rathburn, and L. R. Saslaw. 2012. Effects of grazing and invasive grasses on desert vertebrates in California. The Journal of Wildlife Management 76:670-682.

Glenn, E. and J. Brown. 1998. Effects of soil salt levels on the growth and water use efficiency of *Atriplex canescens* (Chenopodiaceae) varieties in drying soil. American Journal of Botany 85:10-16.

Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. Oecologia 121:518-526.

Hawkes, C. V., We. F. Wren, D. J. Herman, and M. K. Firestone. 2005. Plant invasions alters nitrogen cycling by modifying the soil nitrifying community. Ecology Letters 8:976-985.

Holland, R. F. 1986. Preliminary description of the terrestrial natural communities in California. California Department of Fish and Game, Natural Diversity Database, Sacramento, California.

Jackson, L. E. 1985. Ecological origins of California's Mediterranean grasses. Journal of Biogeography 12:349-361.

Jacobsen, A. L., R. B. Pratt, L. M. Moe, F. W. Ewers. 2009. Plant community water use and invisibility of semi-arid shrublands by woody species in southern California. Madroño 56:213-220.

Keeley, J. E. 2002. Fire and invasive species in Mediterranean-climate ecosystems in California. U.S. Geological Survey, Los Angeles, California. Accessed online at http://www.globalrestorationnetwork.org/uploads/files/LiteratureAttachments/144_fire-and-invasive-species-in-mediterranean-climate-ecosystems-of-california.pdf

Khan, M. A., and We. A. Ungar. 1997. Effects of light, salinity, and thermoperiod on the seed germination of halophytes. Canadian Journal of Botany 75:835-841.

Khan, M. A., and We. A. Ungar. 1984. The effects of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex triangularis* Willd. American Journal of Botany 71:481-489.

Khan, M. A., and We. A. Ungar. 1996. Influence of salinity and temperature on the germination of *Haloxylon recurvum* Bunge ex Boiss. Annals of Botany 78:547-551.

Khan, M., Gul, B., and D. J. Weber. 2004. Temperature and high salinity effects in germinating dimorphic seeds of *Atriplex rosea*. Western North American Naturalist 64:193-201.

Lambrinos, J. G. 2000. The impact of the invasive alien grass *Cortaderia jubata* (Lemoine) Stapf on an endangered Mediterranean-type shrubland in California. Diversity and Distributions 6:217-231.

Leonard, K. J. and L. J. Szabo. 2005. Stem rust of small grains and grasses caused by *Puccinia graminis*. Molecular Plant Pathology 6:99-111.

Mack, R. N. 1986. Alien plant invasion into the Intermountain West: a case history. Ecological Studies 58:191-213.

MacKinnon, E.D., Pratt, R.B. and Jacobsen, A.L., 2014. Functional trait differences between weedy and non-weedy plants in Southern California. Madroño 61:328-338.

Mikhiel, G. S., S. E. Meyer, and R. L. Pendleton. 1992. Variation in germination response to temperature and salinity in shrubby *Atriplex* species. Journal of Arid Environments 22:39-49.

Reinhart, K. O. and R. M. Callway. 2006. Soil biota and invasive plants. New Phytologist 170:445-457.

Sankary, M. N., and M. G. Barbour. 1972. Autecology of *Atriplex polycarpa* from California. Ecology 53:1155-1162.

United States Geological Survey (USGS). 1993. San Joaquin Valley, California. United States Geological Survey. Accessed online at http://pubs.usgs.gov/circ/circ1182/pdf/06SanJoaquinValley.pdf.

Wainwright, C. E., E. M. Wolkovich, and E. E. Cleland. 2012. Seasonal priority effects: implications for invasion and restoration in a semi-arid system. Journal of Applied Ecology 49:234-241.

Wong, L. S., H. H. Aung, M. W. Lame, T.C. Wegesser, and D. W. Wilson. 2011. Fine particulate matter from urban ambient and wildfire sources from California’s San Joaquin Valley initiate differential inflammatory, oxidative stress, and xenobiotic responses in human bronchial epithelial cells. Toxicology in Vitro 25:1895-1905.

Wood, Y. A., T. Meixner, P. J. Shouse, and A. B. Allen. 2006. Altered ecohydrologic response drives native shrub loss under conditions of elevated nitrogen deposition. Journal of Environmental Quality 35:76-92.

Yelenik, S. G., and J. M. Levine. 2011. The role of plant-soil feedbacks in driving native-species recovery. Ecology 92:66-74.

Table 1. Non-parametric contrasts of specific factor levels on soil moisture (m^2 soil/m^2 H_2O) at 10 cm depth between February 2016 and January 2017 at the Environmental Studies Area on campus at California State University, Bakersfield.

Contrast	n	df	*H*	*P*
+RDM vs. -RDM	6	1	0.08	0.771
+RDM vs. +Shade	6	1	41.54	< 0.001
+Weeded vs. -Weeded	9	1	0.91	0.340
Winter vs. Spring 2016	18	1	16.43	< 0.001
Spring vs. Summer 2016	18	1	756.33	< 0.001
Summer vs. Fall 2016	18	1	0.41	0.522
Fall 2016 vs. Winter 2017	18	1	64.24	< 0.001

Table 2. Mean density (individuals/plot) of germination, time (days) to 50% mortality (T50), mean number of survivors, and maximum percent coverage of *Atriplex polycarpa* seedlings per treatment at the Environmental Studies Area on campus at California State University, Bakersfield. Standard errors of the mean are shown in parentheses.

Treatment	Germination[1]	T50	Survival[2]	Max Coverage
+RDM/ -Weeded	0.6 (0.4)	22.2 (4.98)	0	5
-RDM/ -Weeded	6.0 (1.34)	80.7 (8.66)	0.7 (0.1)	50
+RDM/ +Weeded	2.0 (0.62)	21.9 (2.4)	0.7 (0.1)	50
-RDM/ +Weeded	10.1 (2.3)	106 (21.3)	1.0 (0.4)	75
+Shade/ -Weeded	2.3 (0.8)	82.1 (20)	0	25
+Shade/ +Weeded	5.1 (1.2)	87.0 (18)	0.6 (0.24)	50
+RDM Only	1.3 (0.4)	22 (2.1)	0.033 (0.03)	5
-RDM Only	8.1 (1.37)	94.1 (12.1)	0.533 (0.22)	75
+Weeded Only	6.1 (1.4)	78.0 (10)	0.6 (0.2)	50
-Weeded Only	3.3 (0.85)	75.0 (10)	0.022 (0.02)	25
+Shade Only	3.7 (0.75)	85 (13.1)	0.3 (0.13)	50

[1] Mean maximum germination recorded for each plot by treatment in February 2016.

[2] Mean of the number of surviving individuals per plot by treatment in January 2017.

Table 3. Pre-planned contrasts (non-parametric Kruskal-Wallis test) of specific factor levels on the peak germination of *Atriplex polycarpa* seedlings between February 2016 and January 2017 at the Environmental Studies Area on campus at California State University, Bakersfield.

Contrast	n	df	*H*	*P*
+RDM vs. -RDM	60	1	26.51	< 0.001
+RDM vs. +Shade	60	1	23.22	< 0.001
+Weeded vs. -Weeded	90	1	4.720	0.015

Table 4. Pre-planned independent contrasts of specific factor levels on the time in days to 50% mortality (T50) of *Atriplex polycarpa* seedlings between February 2016 and January 2017 at the Environmental Studies Area on campus at California State University, Bakersfield. Data were $\log_{10}$ transformed to satisfy the assumptions of ANOVA.

Contrast	Contrast Mean	MS	df	*F*	*P*
+RDM vs. -RDM	1.14	2.91	29	38.03	< 0.001
+RDM vs. +Shade	0.97	2.07	29	26.97	< 0.001
+Weeded vs. -Weeded	0.17	114.35	44	0.020	0.887

Table 5. Pre-planned independent contrasts (non-parametric Kruskal-Wallis test) of specific factor levels on the vegetative coverage of *Atriplex polycarpa* seedlings at the Environmental Studies Area between February 2016 and January 2017 on campus at California State University, Bakersfield.

Contrast	n	df	*H*	*P*
+RDM vs. -RDM	60	1	4.61	0.032
+RDM vs. +Shade	60	1	6.57	0.010
+Weeded vs. -Weeded	90	1	2.95	0.086

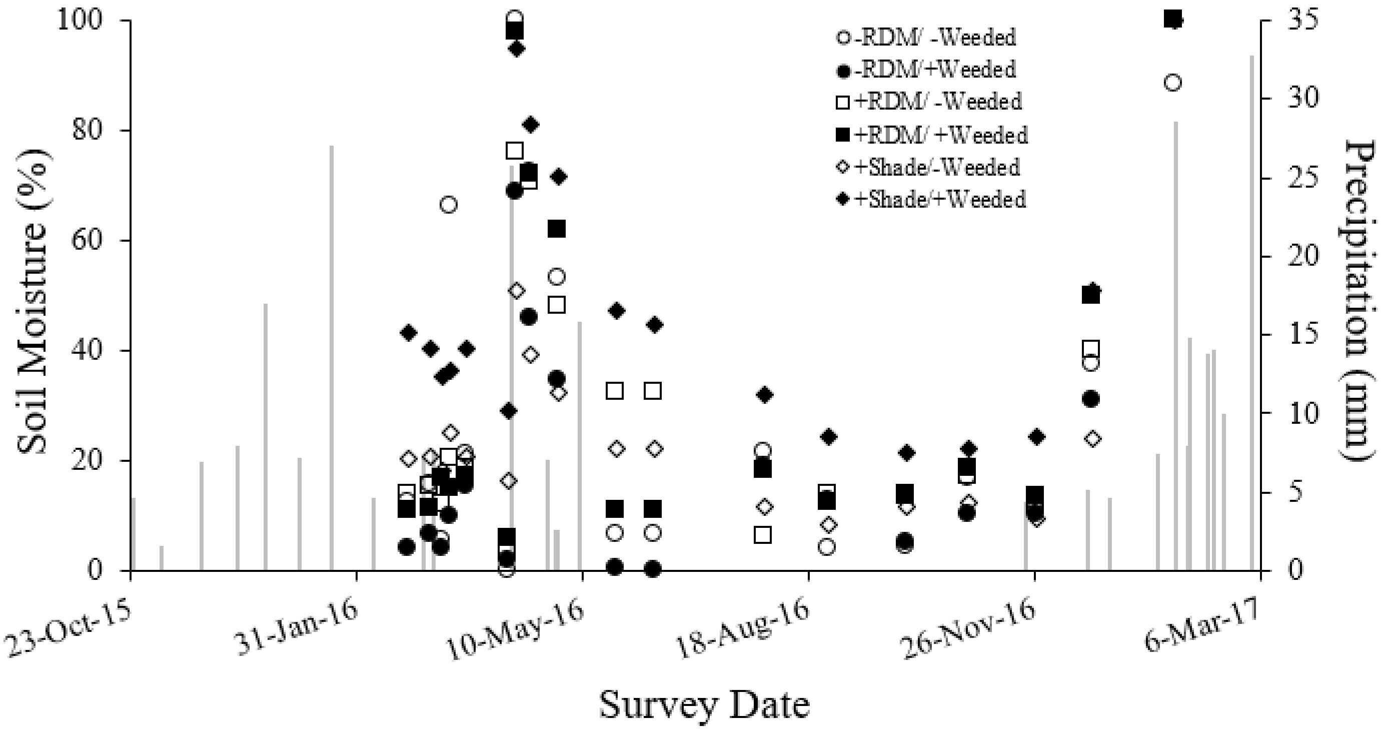

Figure 1. Mean soil moisture by treatment (n = 3 per treatment, expressed as a percentage of maximum) at a depth of 10cm in experimental plots between February 2016 and January 2017 at the Environmental Studies Area on campus at California State University, Bakersfield. Grey bars show precipitation measured on site from October 2015 to March 2017. Error bars are excluded for clarity. RDM = residual dry matter.

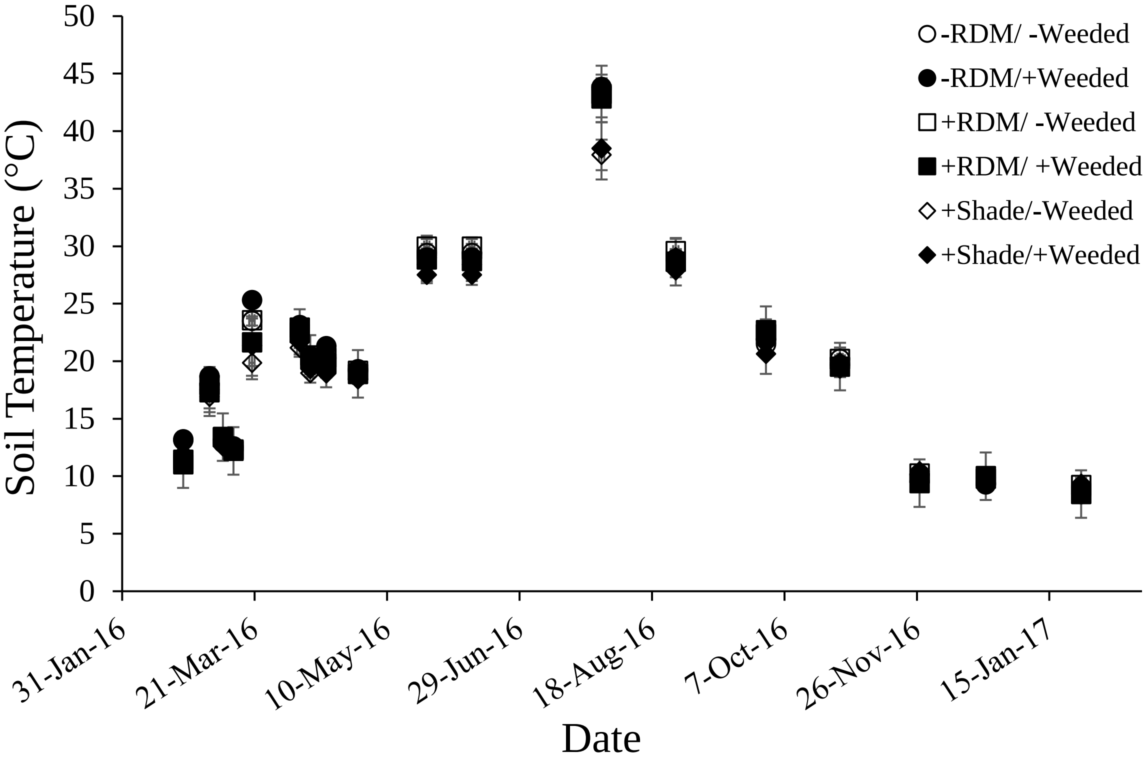

Figure 2. Soil temperature by treatment (n = 3 per treatment) at a depth of 10cm in experimental plots between February 2016 and January 2017 at the Environmental Studies Area on campus at California State University, Bakersfield. Error bars are 95% confidence intervals.

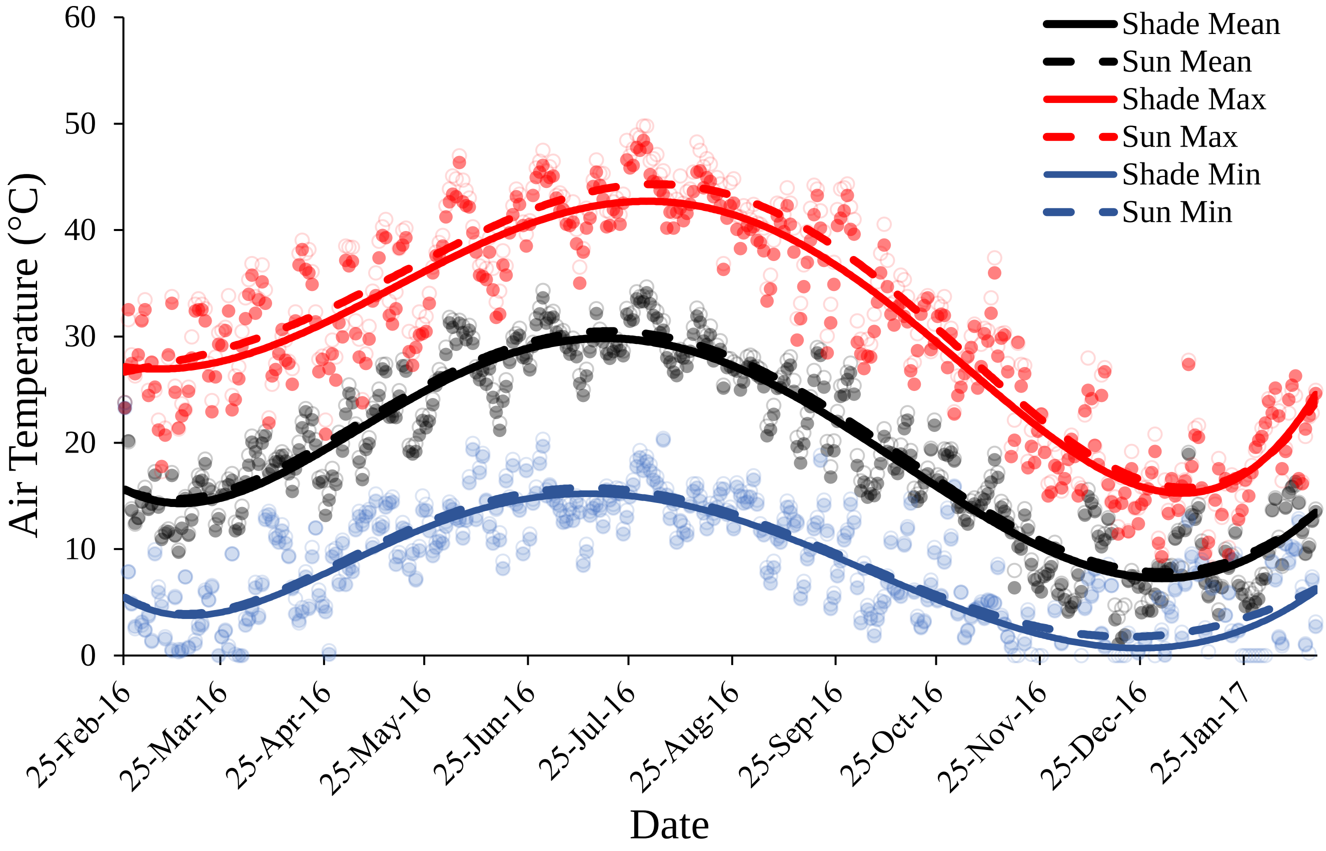

Figure 3. Daily minimum, mean, and maximum air temperatures in full sun (open circles) and underneath shade cloth (closed circles) in February 2016 and January 2017 at the Environmental Studies Area on campus at California State University, Bakersfield. Error bars are omitted for clarity.

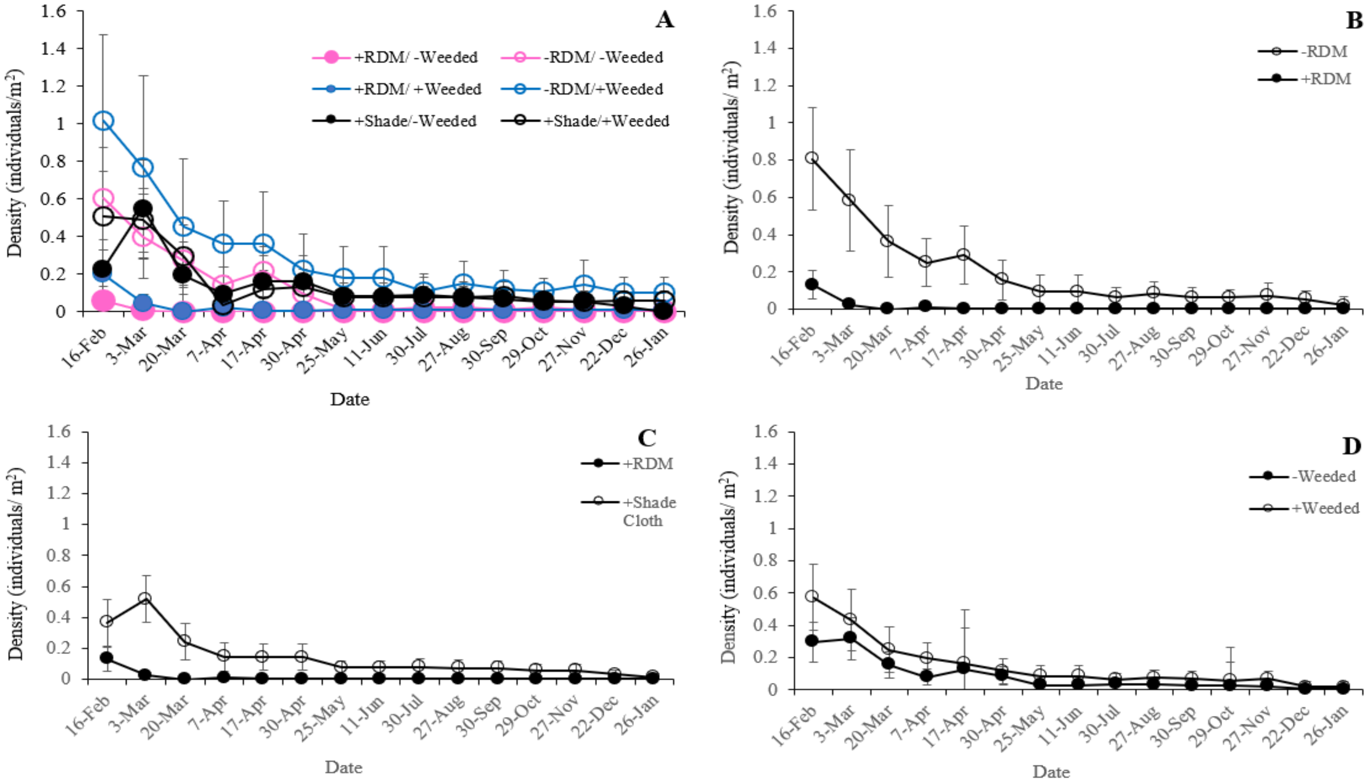

Figure 4. Mean density of *Atriplex polycarpa* seedlings by treatment (n = 15) and treatment level between February 2016 and January 2017 at the Environmental Studies area on campus at California State University, Bakersfield. Error bars are standard errors of the mean.

Chapter 3

Factors affecting seedling recruitment of the native desert shrub *Atriplex polycarpa* (Torr.) S. Watson at Tejon Ranch, California

Mitchell L. Coleman[1], C. Ellery Mayence[2], Michael D. White[2], and R. Brandon Pratt[1]

[1]Department of Biology, California State University, Bakersfield, 9001 Stockdale Hwy,
Bakersfield, California 93311

[2]Tejon Ranch Conservancy, 1037 Bear Trap Road, Frazier Park, California 93243

Abstract

Native saltbush (*Atriplex* spp.) shrubs in the San Joaquin Valley of California have been largely extirpated from the valley floor due to disturbance, invasive species, and habitat conversion. Ecosystem-transforming annual grasses of Mediterranean origin are the chief invaders. Understanding of how these grasses affect saltbush populations is not well established. We hypothesized that saltbush seedling recruitment is limited by the presence of invasive grasses. We predicted that saltbush seedling recruitment would be reduced by resource competition with invasive grasses during the wet season; and structural modification of grass residual dry matter (RDM) formed during senescence. We studied saltbush seedling recruitment in relation to invasive annual grasses in the southern San Joaquin Valley, in the Comanche Point region of Tejon Ranch of California. To test our predictions, we conducted a series of experiments and comparative studies across six isolated stands of saltbush. We assessed the how invasive grasses affect the seedling recruitment of the saltbush *Atriplex polycarpa* (Torr.) S. Watson. We analyzed data with a combination of parametric and non-parametric analyses. Grass RDM reduced saltbush germination compared to plots without RDM. Mortality rate of seedlings was greater in RDM plots than those without; moreover, mortality was 100% for recently germinated seedlings in all plots. Competition with grasses did not affect germination or mortality rate. Saltbush seedlings transplanted into the field had lower mortality and less herbivory in grassy areas compared to seedlings planted in bare zones in between established saltbush shrubs. We conclude that the sites most favorable for saltbush seedling germination are characterized by low grass coverage such as the bare zones common within established saltbush shrubs. Seedling survival is greatest in areas away from established shrubs that are typically characterized by abundant grasses. This creates a seed/seedling conflict, wherein seeds germinate at lower rates in grassy areas, but seedlings survive at higher rates in grassy areas and may explain the limited ability of saltbush stands to expand. Landscape factors leading to differences in water availability, grass invasion, and edaphic characteristics are diverse in the SJV, which also affect saltbush recruitment.

Key Words: valley saltbush shrublands, invasive annual grasses, seedling recruitment, succession.

Introduction

The native upland vegetation of the San Joaquin Valley (SJV) in California is called Valley Saltbush Shrubland (VSS). VSS is an open and low-growing community dominated by shrubs in the family Chenopodiaceae that are commonly called saltbushes. The most common chenopod in VSS is *Atriplex polycarpa* (valley saltbush or saltbush) but other common chenopods include *A. spinifera* J. F. Macbr (spiny saltbush) and *A. lentiformis* (Torr.) S. Watson (big saltbush) (Holland 1986). VSS occurs in upland and moderately saline habitats in the southern and southwestern portions of the SJV and on the Carrizo Plain, along alluvial fans, washes, and hills of the valley floor, mostly on sandy soils with low surface alkalinity (Chatterton 1971, Sankary and Barbour 1972). Commonly occurring adjacent to the shrubs are native and alien annual forbs, as well as abundant invasive annual grasses in the genera *Hordeum*, *Bromus*, *Avena*, and *Shismus* (Holland 1986, Barbour et al. 2007)

Less than 5% of the original range of VSS remains today and the community now occurs mostly in small and isolated remnant patches throughout the SJV (Faber 1997). Some of the last large VSS stands are in the southwestern parts of the valley and on the Carrizo Plain (Holland 1986, Faber 1997, Endangered Species Recovery Program 2015). Most of the destruction has been related to land conversion for agriculture. Preceding VSS destruction has been the nearly ubiquitous invasion of annual grasses native to the Mediterranean-type region of California. The grasses thrive in disturbed areas of the SJV and commonly form large monotypic stands (Bartolome 1979, Jackson 1985, Eliason and Allen 1997, Germano et al. 2001, Corbin and

D'Antonio 2004, Yelenik and Levine 2011). During the dry season, when the grasses die back, the senesced shoots form residual dry matter (RDM). Residual dry matter is a structural modification to otherwise native VSS because it shades the soil, thereby limiting the light level at the soil surface and potentially reducing soil temperature (Bartolome 1979, Eviner 2016).

Mature saltbush shrubs produce thousands of viable seeds during the growing season (September-January) of each year, but most of these seeds do not germinate in areas heavily invaded by annual grasses. Once seeds do germinate, they survive at very low rates (Coleman and Pratt 2017, unpbl.). Thus, the capacity of saltbush to produce established seedlings is ostensibly low in the presence of invasive annual grasses. Microsites that are relatively free from grasses, such as in the bare zones that are commonly observed in the areas in between mature saltbushes, may be important sites for saltbush seedling recruitment.

Previously, we explored how the modification of competition and RDM from invasive annual grasses impact the seeding recruitment of *A. polycarpa* in the SJV (Coleman and Pratt 2017, unpbl.). We found that competition and RDM both affect saltbush recruitment, but RDM was the more important factor and affects saltbush recruitment by suppressing germination and reducing survival. While this previous study was field-based, it was amid an urban environment in a fenced preserve, thus it is possible that the results from that site are not applicable to a more natural field setting. The present study was undertaken to build on the first study to assess if the findings could be generalized to natural sites on Tejon Ranch. The ranch sites contain a broader range of relevant ecological factors that could all affect saltbush seedling success such as the presence of more species of large and medium animals that could affect saltbush populations (e.g. cattle, deer, rabbits, kangaroo rats, and pigs). Moreover, we sampled across sites at the ranch that spanned a range of edaphic and geomorphic characteristics that may be important in affecting saltbush populations. We specifically wanted to address a variety of factors affecting saltbush seed germination and seedling survival (recruitment = germination + survival) in grassy vs. non-grassy areas, as well as how naturally-occurring saltbush seedlings survive over time.

A common observation that has been made of VSS communities is that seedling recruitment occurs in episodic events coinciding with periodic periods of drought (pers. obs.). Past droughts which affected episodic saltbush recruitment events in the SJV may have been important drivers of saltbush demography. However, the demography of VSS is not well understood. One way to determine if populations are expanding, stable, or contracting is to assess the age structure of a population. If a population contains a homogenous mix of ages, it indicates that recruitment is an ongoing process. If the population contains an even age of individuals or is composed of distinct even-aged cohorts, then it indicates that recruitment is likely cued to some critical event such as drought. Such an analysis was timely because recent a drought in California from 2011 to 2016 had diminished invasive grass growth in the SJV and may have contributed to an episodic saltbush recruitment event at Tejon Ranch and throughout the SJV in 2014-2016. Numerous saltbush seedlings germinated throughout the SJV in 2014 in far higher numbers than seen in recent years. It is possible that during years when grass populations perform poorly, such as during drought, that this might make favorable conditions for recruitment. Thus, mature VSS stands likely contain different age classes due to episodic recruitment. Little study has been done of populations of VSS to make inferences about such patterns of recruitment.

We conducted a series of experiments and comparative studies across six VSS sites in the Comanche Point region of Tejon Ranch, California. On a visit to the six sites on 29 January 2016, we found that five of the sites had seedling recruitment in varying degrees, suggesting recent recruitment during the ongoing drought in California. Also, grass populations had been diminished by the drought at this time. We hypothesized that saltbush seedling recruitment would be limited by the presence of invasive grasses. We predicted that saltbush recruitment would be hampered by both invasive grass competition during the growing season and the structural modification of RDM during the dry season. Furthermore, we predicted that distinct cohorts of shrubs in the VSS sites would be identifiable due to past episodic recruitment events, rather than the sites having a even age structure as would be expected if recruitment was consistent year to year. Lastly, we predicted that microsite differences such as edaphic characteristics and water relations between the sites would affect the success of saltbush seedling recruitment.

Methods

Study Area

Tejon Ranch is the largest contiguous parcel of private land in California at approximately 109,265 ha. Our study sites surround Comanche Point in the Tejon Hills region of Tejon Ranch, approximately 8 km southeast of Arvin, California, in the southeast corner of the SJV (Fig. 1). The Tejon Hills are a series of low lying ridges extending north and west from the Tehachapi Range foothills. Comanche Point is located at the northernmost part of Tejon Hills. Geologically, the Tejon Hills are comprised of alluvium sediment layers deposited by rivers draining into the SJV which in the past was an inland ocean (Saleeby and Sams 1987). Millions of years of tectonic shifts, uplifting, and weathering have created unique soils throughout the region that support many rare, endemic, and endangered plant species and are the primary driver for a diverse composition of vegetation types (White and Spiegal 2015). Remnant and isolated stands of VSS can be found around Comanche Point, and because soils are so diverse, it is an especially pertinent area to study saltbush recruitment. The area is also heavily invaded with annual grasses and is continuously grazed by cattle.

We studied *A. polycarpa* because it is a representative shrub of the VSS community and the dominant saltbush species occurring in the VSS sites at Comanche Point. We focused on six separate VSS sites surrounding Comanche Point in an area encompassing 26 km^2 (Fig. 1). The sites experience similar climatic conditions (precipitation, solar irradiance), as well as being at about the same approximate elevation (Table 1). The study region has a diversity of soil types and a range of soil characteristics were quantified (see soil analysis methods below).

We conducted various experiments and comparative studies within and across the six VSS sites at Comanche Point to assess how variations in soil composition, water availability, and ultimately, grass invasion, may affect saltbush seedling recruitment. We used data from a nearby weather station (Fig. 1) for climatic context, including daily temperatures and total precipitation at the time of our study. Climatic data was provided by the Tejon Ranch Conservancy. Weather data in 2016 was available for the entire year, but data for 2017 was available to August 2017. Data for February and March 2017 were unavailable.

Grass RDM and Competition Effects on Seedling Germination and Early Seedling Survival

We tested *A. polycarpa* seedling recruitment by manipulating invasive grass competition and RDM across a series of experimental plot treatments to assess effects on seedling emergence and mortality. The experimental design was repeated from the design described in Chapter 2, although we did not use a shade cloth treatment. We conducted the experiment in a fenced-off exclosure south of Comanche Point (Fig. 1), to ensure that no cattle would disturb the plots during the experiment. The area is heavily invaded with annual grasses.

We established sixty 2 × 5 dm plots were established on 21 December 2016. We randomized plot placement and orientation within the study area, which was approximately 50 × 20 m of flat area in Comanche Point with uniform environmental conditions and dominated by invasive annual grasses. We cleared each plot of vegetation by raking away the previous year's RDM and hand weeding where necessary. We marked and anchored the plots with numbered pin flags at each corner to ensure the same area was surveyed over the course of the study. We sowed seeds of *A. polycarpa* were then sown in the plots (100 seeds per plot) and randomly spread with a rake. Invasive grass competition and RDM were manipulated with the following treatments: 1) RDM was either directly added to a specified amount or not added (+/- RDM); and 2) plots were either weeded or unweeded to test competition (+/- weeded). We randomly assigned each plot to one of four treatments (n = 15 plots/ treatment): 1) +RDM/ -Weeded, 2) -RDM/ -Weeded, 3) +RDM/ +Weeded, 4) -RDM/+Weeded.

We standardized he amount of RDM added to +RDM plots by adding RDM until the light level (400-700nm) at the soil surface underneath the RDM was approximately 300 µmols of quanta m^{-2} s^{-1} measured on a clear sunny day at noon (ambient PPFD ~ 2000 µmols quanta m^{-2} s^{-1}; Li 250A, Li-Cor Corporation, Lincoln, Nebraska, USA). This light level corresponded to the amount of shade produced from the moderately dense RDM on site at noon. On a dry mass basis, the mean amount of applied RDM was approximately 0.0015 kg/m^2, which was comparable to densely invaded old-field areas throughout the SJV (Bartolome et al. 2002). The RDM added to the plots came from on site. It consisted primarily of shoots of *Avena sativa* L. and *Bromus diandrus* Roth. When weeding, we avoided disturbing *A. polycarpa* seeds and seedlings in the plots. This was best accomplished by frequent visits to the site when the grasses and forbs were just germinating (January – March) so they could be removed when recently germinated and very small. We weeded plots as necessary at the same time as plot measurements.

To determine effects of the treatments, we measured *A. polycarpa* density (individuals/ plot) from 20 February 2017 (right after germination) to 26 April 2017. We used a 2 × 5 dm plot that was color coded to collect the data (Daubenmire 1959). Measurements were made approximately every other week after initial germination in the winter and spring of 2017 to capture the rapid germination and mortality that occurred during that time (February-April).

Survival of Transplanted Seedlings in Native VSS vs. Invasive Grassland

The isolated VSS stands at Tejon Ranch are small and abruptly give way to invaded grassland habitat that is immediately adjacent to the shrubs. It is possible that these small areas are of a type uniquely suited to saltbush and that the adjacent grass habitat is somehow unsuitable to the shrubs. This could be related to edaphic factors that are heterogeneous around the study area. To test this possibility, we planted seedlings into two sites currently occupied by saltbushes and adjacent grasslands and monitored their size, herbivory, and survival over time.

To propagate seedlings for this experiment, we collected seeds of *A. polycarpa* and native soil from two sites (sites 3 and 4, Fig. 1) on 29 January 2016. On 14 April 2016, and sowed the seeds in the native soil in shallow flats 40 × 20 cm and 1 cm deep in a greenhouse on campus at CSU Bakersfield and irrigated for 10 minutes once per day. Once germinated, we planted the seedlings in individual tree tubes and moved them outdoors. We watered the seedlings once per week from May to October 2016 but stopped watering between November 2016 and January 2017. The seedlings were twice fertilized at one-quarter the recommended amount once in July 2016 and once in November 2016 (Miracle-Gro All Purpose Plant Food, Model # 100123, Scotts Miracle-Gro Company, Marysville, Ohio). On 20 January 2017, after rains had wetted the soil and at a time when seeds would be germinating in the field, we planted the seedlings at the two sites at Comanche Point. We chose to transplant into these two sites specifically because both are relatively uninvaded with annual grasses within the stand of saltbushes, but also because they have nearby adjacent areas of invasive annual grassland that could be planted into.

We equally divided 152 seedlings between the two sites. At each site, we transplanted half of the seedlings (n = 38) into native VSS habitat and the other half into adjacent invasive grassland. We oriented seedlings in each treatment in a single transect in an East/ West orientation (bearing 240°) for each treatment, spaced 1m apart, and watered in with 500 mL of water at the time of planting. We randomly determined the placement of transects by tossing a colored marker and establishing a transect at the point of landing. We repeatedly measured the growth (height in cm) and survival (alive vs. dead) of each seedling once per month until 4 October 2017. We also noted incidences of herbivory and causes of death when possible.

Native Seedling Survival

We tagged 250 naturally occurring saltbush seedlings across all five of the sites (Fig. 2: sites 1, 3, 4, 5, and 6) on 3 May 2016 and repeatedly sampled for survival (dead vs. alive) until 4 October 2017 (site 2 had no seedlings in 2016). In total, we tagged 67 seedlings at site 1, 63 and site 3, 40 and site 4, 40 at site 5, and 40 at site 6. We tagged different numbers of seedlings at each site because seedlings tended to occur in clusters at the base of some adult shrubs rather than uniformly spread throughout each site. Furthermore, the seedlings were tagged within the radius of a demographic survey area at each site (described below). The seedlings were tagged at their base with loosely fitting zip ties, approximately three months after initial germination in February 2016. We did not tag established seedlings older than three months (i.e. from the previous year).

Size Class Analysis to Estimate Demography

We conducted a demographic study of the six VSS sites surrounding Comanche Point (Fig. 1, sites 1-6) to assess age differences within and between sites. All measurements were taken between May and December of 2016 prior to seasonal rains. Saltbush produces secondary anomalous growth lacking clear growth rings, is multi-stemmed, and often experiences dieback of branches; therefore, there is no reliable way to date the age of saltbush in the field (Fahn and Zimmermann 1982). A common alternative approach is to use size as a proxy for age (Leftkovitch 1965); therefore, we measured size (canopy volume) as a proxy for age. Thus, canopy volume comparisons of *A. polycarpa* individuals within and between the six VSS stands allowed us to approximate if the stands are of even or mixed age. We assumed that adult shrub size is related to age: that small shrubs are young, and large shrubs are old.

At each site, we marked a central survey point by tossing a colored marker and placing the point of the plot where it landed. From the central point, all shrubs were measured within a thirty-meter radius, starting clockwise from 0° north. We used tape measures and meter sticks to measure crown width (the shrub crown interval along the transect from the central point), cross width (the width perpendicular to crown width), and height in m of each shrub within the radius. We then used the crown width, cross width, and height to calculate the canopy volume (CV) in m^3 of each shrub with the following formula from Thorne et al. (2002):

$$CV = 2/3\ \pi \text{ x height x } [(\text{crown width}/2) \times (\text{cross width}/ 2)]$$

Site Differences

We sampled across a diverse set of six field sites on Tejon Ranch. We made a wide range of measurements related to water availability (water potential of plants and soils), soil characteristics (texture and chemistry), and biotic differences such as the amount of grass.

Seasonal Water Potential

We measured midday branchlet water potentials (Ψ_w) from outer canopy (sun-exposed) and south-facing sides of the same three adult shrubs per site in the winter (February 21, maximal site moisture) and fall (October 4, most limited moisture) of 2017 to assess patterns of water available to shrubs at the different sites. This gave an estimate of the soil water that was available to the plants across sites. Values are also affected by plant water use (transpiration rates at the time of sampling) and the hydraulic conductivity of the soil and plant. On both sampling periods, the weather was sunny, and samples were harvested between 1130 and 1230. Three shrubs were randomly selected per site were by tossing a colored marker and assigning a number to the closest shrub at the point of landing. We clipped three branchlets from each shrub (subsamples), bagged, and placed into a cooler with ice packs (n = 3 samples and 3 subsamples per site per season). We then transported the samples back to the lab at CSU Bakersfield and water potentials were measured with a pressure chamber (Model 2000 Pressure Chamber Instrument, PMS Instruments, Corvalis, Oregon, USA) within 3 hours of removal. Concurrent with branchlet water potential measurements, we collected soil samples from various depths (surface, 10cm, 20cm, 50 cm, and 100cm) at each site and measured for soil water potential with dew point hygrometers (WP4C water potential meter, Decagon Devices, Pullman, Washington, USA) to assess soil moisture differences at different soil depths.

Soil Composition

We collected three 10 cm soil cores from each of the six VSS sites. We randomly chose each core location by blindly tossing a colored marker. We then homogenized the three samples from each site (n = 1 sample per site) and conducted soil analyses. Soil samples were sent Utah State University Analytical Labs (USUAL) to measure soil pH, salinity, texture, available phosphourous, available potassium, available nitrogen, sulfate, DTPA- extractable metals (zinc, iron, copper, and manganese), and the percentage of organic matter.

Methods used by the lab were standard ones and we only briefly mention here an overview of the methods. Soil pH was measured with saturated paste with a pH meter, and salinity with saturated paste with an electrical conductivity probe (Mclean 1982). Nitrate (available soil N) was measured with the $CaOH_2$ extraction method, using colorimetric determination with chromotropic acid (Sims and Jackson 1971). Soil texture was determined by feeling using the USDA Soil Texture Triangle and NRCS Guide (Thien 1979). Available potassium and phosphorous were measured by sodium bicarbonate extract using ascorbic acid with molybdate blue as a colorimetric (Olsen and Sommers 1982) with a Thermo Electron Solar S2 AA (Atomic Absorption Spectrophotometer). DTPA-extractable metals were measured with ICP assays (Lindsay and Norvell 1978). Sulfate was measured with the $CaHPO_4$ extraction method (Lindsay and Norvell 1978). The amount of organic matter was measured with the Walkey-Black assay (Nelson and Sommers 1982).

Lastly, the percentages of various soil minerals at each site were analyzed with x-ray-diffraction (Boski et al. 1998, Underwood and Guo 2013). We collected soil samples on 4 October 2017 at peak dry conditions and quickly analyzed for mineral composition. We analyzed the samples in both bulk and clay-sized fractions separately from soil samples described above with x-ray diffraction (PANalytical Empyrean X-Ray Diffractometer, Lelyweg, The Netherlands).

Grass Invasion

We quantified the level of grass invasion between adult saltbush shrubs at each site on 20 February 2017 by randomly and repeatedly tossing a colored marker and measuring the percentage of grass coverage at each spot were the marker landed (n = 30 plots). We used a 2 x 5 dm plot that was color coded to aid in rapid collection of percent coverage (Daubenmire 1959). We determined percent coverage by analyzing the total percentage of ground covered by invasive grasses within each plot, then assigning each species the appropriate percentage to the nearest integer in increments of five. We took all measurements within the 30-meter radius of the demographic analysis at each site (see above).

Statistical Analyses

We conducted statistical analyses using non-parametric methods outlined in Barnard et al. (2007) and implemented in in Microsoft Excel (Microsoft Corporation, Bellingham, Washington, USA), JMP 13™ (SAS Institute, Cary, North Carolina, USA) and/ or Minitab 18™ (Minitab Inc., State College, Pennsylvania, USA). Type I error rate was set at 0.05 for all comparisons. All data were checked for normality and constant variance and were transformed as necessary. In some cases, transformations failed, and non-parametric models were used.

Grass RDM and Competition Effects on Seedling Germination and Early Seedling Survival

We assessed the density of *A. polycarpa* (count of individuals/ plot) in a manner to capture key aspects of the response to the treatments that included the peak density within each plot, which represented the amount of germination of the original 100 seeds added to each plot (Kruskal-Wallis test). A second analysis was the time to 50% mortality (time in days to density at 50% reduction from peak density within each plot) that estimated mortality rate. This analysis was done by calculating the slope of the relationship between seedling density plotted over time for each plot and treatment. We omitted plots with less than three linear points (i.e., with little or no germination) from the regression. We analyzed time to 50% mortality was across the treatments with a Kruskal-Wallis test. We used pre-planned independent contrasts to test for differences between individual factor levels (+RDM vs. -RDM and +weeded vs. -weeded plots).

Native Seedling Survival

To assess variable levels of survival between of the tagged saltbush seedlings, we used a general linear model ANOVA with a binomial response (dead vs. alive). We used survival data from 4 October 2017 to assess differences across sites.

Demography

To assess variation in canopy volume of the various sites, we analyzed both differences between the sites with Kruskal-Wallis tests. Pre-planned contrasts were used to test for differences between specific sites.

Survival of Seedlings Transplanted into Native VSS vs. Invasive Grassland

We assessed the total number of surviving individuals as of 4 October 2017 by site (n = 2, sites 3 and 4) and by treatment (grassland vs. saltbush) with heterogeneity chi square tests with the Yate’s correction. We used an expected value of 19 (n = 38/2) pertaining to the null hypothesis that survival would not differ by treatment and would be 50%. A second null hypothesis was that survival would not vary by site.

Seasonal Water Potential

We assessed variations in branchlet water potentials by season and site with a two-way ANOVA. An interaction term between site and season was included in the model. Both site and season were used as fixed factors. Pre-planned contrasts were used to assess site-specific variations.

Grass Invasion

We assessed differences in the level of grass invasion between the six sites with a one-way ANOVA. Pre-planned contrasts were used to assess specific site differences.

Results

Precipitation and Temperatures

The total amount of precipitation at Comanche Point in 2016 was 177.8 mm, greater than the yearly regional average. Precipitation in December 2016 alone was 63.75 mm, which was enough water to saturate all the VSS sites at Comanche Point with water (see below). The amount of precipitation in early 2017 was not as high as December 2016. Temperatures registered throughout 2016 and 2017 were consistent with regional averages (Fig. 2).

Grass RDM and Competition Effects on Seedling Germination and Early Seedling Survival

Peak *A. polycarpa* germination varied among the treatments (H = 17.85, df = 3, P = 0.005; Fig. 3). The presence of RDM reduced the germination of seedlings compared to the -RDM treatment (H = 16.98, df = 1, P < 0.001). Competition for resources from the invasive grasses did not impact germination (H = 0.39, P = 0.533). Time to 50% mortality also varied by treatment (H = 11.1X, df = 3, P = 0.011; Fig. 3). The presence of RDM increased the rate of mortality (H = 4.77, df = 1, P = 0.028) when compared to plots with no RDM. Competition for resources did not influence mortality rate (H = 0.75X, df = 1, P = 0.387). All seedlings suffered mortality during this experiment by April 2017, that is, no seedlings survived from the surveyed cohort.

Survival of Planted Seedlings

Heights of transplanted saltbush seedlings varied by site and treatment (Fig. 4A). At site 3 in October 2017, 11 of 38 planted saltbush seedlings were still alive in the native VSS habitat while 27 of 38 were alive in the grassland (Fig 4B). At site 4, eight survived in native VSS while 20 survived in the grassland. Saltbush seedlings survived at lower rates when planted among saltbush shrubs compared to those planted among invasive annual grasses ($\chi^2 = 10.98$, df = 1, $P < 0.05$). The number of surviving seedlings also varied by site ($\chi^2 = 48.191$, df = 1, $P < 0.05$). Seedling mortality among saltbushes appeared to be due to herbivory from small mammals. We did not observe herbivory as a source of mortality for seedlings growing in the grassland treatment (Fig. 4B). Of 250 tagged seedlings in May 2016, 173 perished by October 2017 ($\chi^2 = 308.4$, df = 248, $P = 0.005$; Table 2).

Demography

Age of shrubs was estimated by measuring their size (canopy volume) at each site. The sites differed in their apparent age ($H = 73.18$, df = 5, $P < 0.001$; Fig. 5, Table 3). There were no large (> 15 m^3) shrubs on sites 3, 4, as was observed at site 6, whereas there were a few large plants on sites 1, 2, and 5. All sites had small individuals, but numbers differed (Fig. 5). The average size of shrubs at sites 2 and 5 were significantly larger than at the other four sites ($H = 16.98$, df = 1, $P <0.001$), but did not differ significantly between these sites ($H = 0.20$, df = 1, $P = 0.655$). Shrubs at site 1 were significantly larger than those at sites 3, 4, and 6 ($H = 197.12$, df = 1, $P < 0.001$), shrubs at site 6 were significantly larger than at site 3 ($H = 6.38$, df = 1, $P = 0.010$) and site 4 ($H = 4.29$, df = 1, $P = 0.040$), and shrubs at site 4 were significantly smaller than at site 3 ($H = 11.91$, df = 1, $P < 0.001$; Table 3).

Site Differences

Branchlet water potentials varied by season (winter wet and fall dry) and by site. There was an interaction between site and season, as all sites did not respond the same across the two seasons (Table 4, Fig. 6). Site 2 had a lower minimum value (fall) than some of the others (site 1 and 4) indicating that, at this site, the shrubs had less water available to them. Soil moisture varied by site, with site 4 standing out as the most unique. The soil moisture at site 4 was drier at depth in the winter, but retained more moisture at depth during the summer, compared to the other sites that were more similar across the seasons (Fig. 7). The winter branchlet water potential from site 4 matched the winter soil moisture at that site; the soil was drier at depth (> 0.5 m), and had a lower branchlet water potential, compared to the other sites.

The sites varied in soil composition (Table 5). Site 4 was the most saline of all the sites and had the highest levels of available nitrogen, phosphorous, and sulfate. Available potassium was the highest at site 5. Soil texture was similar at sites 3, 5, and 6, which each had a sandy loam texture. Sites 1 and 4 had a sandy clay loam texture whereas site 2 had loamy sand. Each of the sites did not substantially vary in pH or the percentage of organic matter. DTPA-extractable metals also varied by site. Mineral assemblages in bulk soil samples varied in composition and relative equitability. Clay mineral contents between the sites also varied in composition and type of clay minerals. The level of invasive grass coverage in February 2017 varied significantly by site ($F_{1,5} = 80.36$, $P = 0.004$; Table 1).

Discussion

Grass RDM and Competition Effects on Seedling Germination and Early Seedling Survival

We hypothesized that invasive grass competition and RDM would be key factors affecting saltbush recruitment. Our results suggest that saltbush germination was reduced by RDM to a significant degree. We also found that survival of germinated seedlings was zero in all treatments, indicating that seedling survival is an important bottleneck in saltbush populations. This result, at a more natural field site than the one previously studied in Chapter 2, reinforces the interpretation of saltbush life history as one wherein shrubs produce thousands of seeds each year, but relatively few germinate and even fewer survive beyond the first three months. This effect on germination may prevent ecological succession of invasive grasslands to VSS and is consistent with our previous result (Chapter 2).

There were some differences between this study and the previous one. Competition with invasive grasses can play a role in influencing saltbush recruitment, but at the Tejon plots, RDM acted solely to affect germination and mortality rate, whereas competition did not have a significant effect. Also, the survival was lower in the Tejon field plots compared to the plots on campus at CSU Bakersfield. Seedlings in the field died *en masse* in early April 2017, whereas some seedlings on campus survived through the summer and into the following winter as established seedlings. This wholesale die-off suggests a common cause and one likely factor is the relatively dry conditions due to a virtual lack of precipitation from February to April 2017. The lack of rainfall for two and a half months prior to the April die-off may have resulted in lack of water to the small and establishing seedlings. This was not the case for my previous study where there was a more even rainfall pattern in the winter that may have provided adequate moisture to keep seedlings alive (Coleman and Pratt 2017, unpbl.).

Seedling Survival in Native VSS vs. Invasive Grasslands

Isolated stands of VSS may occupy presently suitable habitat and seedlings may not be able to colonize grassy areas because the habitat is somehow unsuitable. This hypothesis was not supported by our seedling transplant experiment. While germination of saltbush seedlings was negatively affected in grassy areas by RDM, transplanted seedlings in grassy areas had higher rates of survival than those transplanted into saltbush areas. In this experiment, survival of seedlings after three months was lower in bare areas in between mature saltbush shrubs compared to seedlings planted in grassy areas. Herbivory appeared to be the chief agent of mortality for saltbush seedlings among the saltbush adults, whereas mortality in the grassy areas was due to unknown causes but did not appear to be related to herbivory. Considering this in relation to the results of the competition/ RDM experiment, it would suggest a seed-seedling conflict, wherein saltbush seeds germinate optimally in open areas without inhibition by invasive grass RDM and competition, but established seedlings survive at lower rates in bare areas among saltbush adults.

Demography

We observed that shrubs varied size by site, and all sites had a wide heterogeneity of shrub canopy volumes. The suite of shrub sizes present at each site suggests that saltbush recruitment events are generally not consistent from year to year but rather occur in distinct flushes, perhaps coinciding with significant climate perturbations such as long term, high intensity droughts. We observed one such recruitment event in the winter and spring of 2016, just as we were beginning to assess the demographic makeup of each site. The observed variability in apparent shrub age is consistent with episodic recruitment events. We assumed that age of saltbush shrubs is related to size, though site differences in edaphic composition, soil water availability, midday branchlet water potentials, and foliar dieback may affect shrub size, particularly when compared across sites.

The Role of Site Differences in Saltbush Demography, Invasibility, and Seedling Survival

We found that soil composition varied by site in ways that are likely important to saltbush populations and may be related to moisture available to saltbushes. Saltbushes differed in branchlet water potentials across the sites suggesting that some sites were characterized by less available water. The differences in water availability at the sites may also explain the degree of grass invasion at the sites. The different sites had different levels of grass invasion and adult shrub health. Edaphic factors indirectly and directly influence the performance of saltbush at the various sites by controlling the amount of water available to adult shrubs (thus impacting branchlet water potentials and the amount of foliar dieback). A consistent pattern we observed throughout out study was that site number 4 varied from the other five sites: it had lower soil moisture availability, lower midday branchlet water potentials, younger and less variable demographic composition (smaller and more uniform shrub sizes compared to the other sites), and lower seedling survival (fewer planted saltbush seedlings survived in site 4 compared to site 3).

In February 2017 (the critical time for saltbush germination), we found that all six sites had consistent surface moisture but varied between the sites at depth. Rainfall events in December and January saturated the surface soils with water throughout Comanche Point. In the context of germination for both saltbush and invasive grasses, surface soil moisture is essential and did not vary but site; therefore, it may not have been a cause of the observed site variability in germination of seedlings in February 2016.

Synthesis

We found that there are multiple of factors controlling the recruitment of saltbush in the SJV. Saltbush seeds and seedlings perform more poorly in areas heavily invaded by invasive annual grasslands. Specifically, the RDM from previous years acts to inhibit saltbush germination to a degree that would seem to prevent ecological succession of invasive grassland to VSS. By contrast, seedlings, once relatively well-established, perform best in open grassland environments by avoiding herbivores in mature saltbush stands. This creates a mismatch where seeds are most likely to germinate in bare zones near established shrubs, and seedlings are most likely to survive in grassy areas. Such seed-seedling conflicts have been previously described (Lamont et al. 1993, Schupp 1995, Germano et al. 2001).

Acknowledgements

We thank Dr. Anna Jacobsen and Dr. David Germano of California State University, Bakersfield (CSUB), for their substantive comments and advice which greatly improved the quality of the manuscript. We also thank the Educational Partnership Impacting Colleges and Careers (EPIC) between CSU Bakersfield, Mrs. Gayle Batey, and the Tejon Ranch Conservancy for providing funding, logistical support, and site access which enabled us to carry out this research at Tejon Ranch. We also thank the National Science Foundation (NSF) Center for Research Excellence in Science and Technology (CREST) (HRD-1547784) grant for funding this research. We also thank Dr. Adam Guo and Morgan Kayser of the CSUB Geology Department for helping us to analyze the soil samples. We also thank Alex Baer, Eva Arrieta, and Logan Salazar for assisting with data collection in the field.

Literature Cited

Bajji, M., J. M. Kinett, and S. Lutts. 2002. Osmotic and ionic effects on NaCl on germination, early seedling growth, and ion content of *Atriplex halimus* (Chenopodiaceae). Canadian Journal of Botany 80:297-304.

Baker, J. B., R. J. Southard, and J. P. Mitchell. 2005. Agricultural dust production and standard conservation tillage systems in the San Joaquin Valley. Journal of Environmental Quality 34:1260-1269.

Barbour, M., T. Keeler-Wolf, and A. Schoenherr. 2007. Terrestrial Vegetation of California, 3rd Edition. University of California Press. Berkeley, California.

Beisner, B. E., D.T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1:376-382.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J. W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., de Vries, W. 2010. Global aaessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological Applications. 20:30-59.

Boski, T., Pessoa, J., Thorez, J., Dias, J.M.A., and We. R. Hall. 1998. Factors governing abundance of amino acids in the sediments from the N.W. European Continental Margin. Progress in Oceanography 42:145-164.

Brown, J., K. Benedict, B. J. Park, and G. R. Thompson. 2013. Coccidioidomycosis: epidemiology. Clinical Epidemiology 5:185-197.

Chatterton, N. J., J. R. Goodin, C. M. Mckell, R. V. Parker, and J. M. Rible. 1971. Monthly variation in the chemical composition of desert saltbush. Journal of Range Management 24:37-40.

Chow, J. C., J. G. Watson, D. H. Lowenthal, P. A. Solomon, K. L. Magliano, S. D. Ziman, and L. W. Richards. 1993. PM10 and PM2.5 compositions in California's San Joaquin Valley, Aerosol Science and Technology, 18:2, 105-128.

Daubenmire, R. F. 1959. Plants and environment: a textbook of plant autecology. John Wiley and Sons Inc., New York, New York.

De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology 72:1076-1088.

Dodd, G. L., and L. A. Donovan. 1999. Water potential and ionic effects on germination and seedling growth of two cold desert shrubs. American Journal of Botany 86:1146-1153.

Eviner, V. T. 2016. Grasslands. Pages 449-477 in Ecosystems of California. Mooney, H., and E. Zavaleta, editors. University of California Press. Oakland, California.

Faber, P. 1997. California’s Wild Gardens:A Guide to Favorite Botanical Sites. University of California Press. Berkeley and Los Angeles, CA.

Fahn, A., and M. H. Zimmermann. 1982. Development of the successive cambia in *Atriplex halimus* (Chenopodiaceae). Botanical Gazette 143:353-357.

Germano, D. J., G. B. Rathburn, and L. R. Saslaw. 2001. Managing exotic grasses and conserving declining species. Wildlife Society Bulletin 29:551-559.

Germano, D. J., G. B. Rathburn, and L. R. Saslaw. 2012. Effects of grazing and invasive grasses on desert vertebrates in California. The Journal of Wildlife Management 76:670-682.

Glenn, E. and J. Brown. 1998. Effects of soil salt levels on the growth and water use efficiency of *Atriplex canescens* (Chenopodiaceae) varieties in drying soil. American Journal of Botany 85:10-16.

Holland, R. F. 1986. Preliminary description of the terrestrial natural communities in California. California Department of Fish and Game.

Jackson, L. E. 1985. Ecological origins of California's Mediterranean grasses. Journal of Biogeography 12:349-361.

Khan, M. A., and We. A. Ungar. 1984. The effects of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex traingularis* Willd. American Journal of Botany 71:481-489.

Khan, M. A., and We. A. Ungar. 1996. Influence of salinity and temperature on the germination of *Haloxylon recurvum* Bunge ex Boiss. Annals of Botany 78:547-551.

Khan, M., Gul, B., and D. J. Weber. 2004. Temperature and high salinity effects in germinating dimorphic seeds of *Atriplex rosea.* Western North American Naturalist 64:193-201

Lamont, B. B., Witowski, E. T., and N. J. Enright. 1993. Post-fire litter microsites: safe for seeds, unsafe for seedlings. Ecology 74:501-521.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1-18.

Lindsay, W. L. and W.A. Norvell. 1978. Development of a DTPA soil test for zinc, manganese, and copper. Soil Science Society of America 42:421-428.

Malmstrom, C. M., A. J. McCullough, H. A. Johnson. L. A. Newton, and E. T. Borer. 2005. Invasive annual grasses indirectly increase virus incidence in California native perennial bunchgrass. Oecologia 145:153-164.

Mandak, B. 2003. Germination requirements of invasive and non-invasive *Atriplex* species: a comparative study. Flora 198:45-54.

Mclean, E. 1982. Soil pH and lime requirement. Methods of soil analysis, Part 2. Agronomy 9:199-224.

Meng, Y., Rull, R., Wilhelm, M., Lombardi, C., Balmes, J., and R. Beate. 2009. Outdoor air pollution and uncontrolled asthma in the San Joaquin Valley, California. Journal of Epidemiological Community Health 64:143-147.

Mikhiel, G. S., S. E. Meyer, and R. L. Pendleton. 1992. Variation in germination response to temperature and salinity in shrubby *Atriplex* species. Journal of Arid Environments 22:39-49.

Nelson, D. W. and L.E. Sommers. 1982. Total carbon, organic carbon, and organic matter. Soil analysis, Part 2. Agronomy 9:539-580.

Philips, S., Kelly, P., Williams, D. California State University, Stanislaus. 2015. Endangered Species Recovery Program (ESRP). Accessed online at https://databasin.org/datasets/9d98c56b03104a4386cc8858ebfea031.

Saleeby, J. B., and D. B. Sams. 1987. U/Pb zircon, strontium, and oxygen isotopic geochronology study of the southernmost Sierra Nevada batholith, California.

Sankary, M. N. and M. G. Barbour. 1972. Autecology of *Atriplex polycarpa* from California. Ecology 53:1155-1162.

Lindsay, W. L. and W.A. Norvell. 1978. Development of a DTPA soil test for zinc, iron, manganese, and copper. Soil Science Society of America 42:421-428.

Schupp, E.W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 10:399-409.

Sims, J.R., and G.D. Jackson. 1971. Rapid analysis of soil nitrate with chromotropic acid. Soil Science Society of America 35:603-606.

Thien, S. J. 1979. A flow diagram for teaching texture by feel analysis. Journal of Agronomic Education. 8:54-55.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81-92.

Underwood, M. B. and J. Guo. 2013. Data report: clay mineral assemblages in the Shikoku Basin, NanTroSEIZE subduction inputs, IODP sites c0011 and C0012. Proceedings of the integrated ocean drilling program 322.

Van Der Heijden, Marcel. 2004. Arbuscular mycorrhizal fungi as support systems for seedling establishment in grassland. Ecology Letters 7:293-303.

White, M., and S. Spiegal. 2015. Managing grasslands on Tejon Ranch: the ecological site concept. Grasslands 25:1-5.

Wong, L. S., H. H. Aung, M. W. Lame, T.C. Wegesser, and D. W. Wilson. 2011. Fine particulate matter from urban ambient and wildfire sources from California's San Joaquin Valley initiate differential inflammatory, oxidative stress, and xenobiotic responses in human bronchial epithelial cells. Toxicology in Vitro 25:1895-19.

Table 1. Site characteristics of six saltbush (*Atriplex polycarpa*) stands located in the Comanche Point region of Tejon Ranch in the San Joaquin Valley of California. Geographic coordinates served as the central survey point for a demographic analysis of each site. Coverage of invasive grasses represent mean grass levels observed at each site on 20 February 2017 (n = 30 measurements per site). Standard errors of the mean are shown in parentheses.

Site Number	Latitude (N)	Longitude (W)	Altitude (m)	Slope/ aspect	Grass Coverage (%)
1	35° 5' 30.984"	118° 48' 36.3564"	226	20°/ west facing	60.4 (8.2)^{A}
2	35° 5' 33.0144"	118° 49' 9.6168"	233	flat	35.1 (4.6) ^{B}
3	35° 8' 8.9736"	118° 49' 55.7112"	162	35°/ west facing	18.4 (9.3)^{C}
4	35° 8' 18.114"	118° 49' 29.2692"	167	30°/ west facing	6.4 (1.9)^{D}
5	35° 7' 52.554"	118° 48' 47.9268"	184	flat	71 (8.3)^{A}
6	35° 9' 49.4964"	118° 47' 45.2184"	172	45°/ southwest facing	4.3 (0.76)^{D}

*superscripted letters denote statistical similarity or differences in grass invasion between sites.

Table 2. Survival and mortality of naturally occurring saltbush (*Atriplex polycarpa*) seedlings tagged across five sites in the Comanche Point region of Tejon Ranch in the San Joaquin Valley of California. We tagged 250 seedlings were tagged in May 2016 and monitored for survival until October 2017. There were no seedlings at site number 2.

Site Number	Number of Seedlings Tagged	Number of Survivors	Percent Mortality
1	67	15	78
3	63	29	54
4	40	5	88
5	40	25	40
6	40	3	92
Total	250	77	70

Table 3. Shrub characteristics of six saltbush (*Atriplex polycarpa*) sites at the Comanche Point region of Tejon Ranch in the San Joaquin Valley of California. All shrubs within a thirty-meter radius were measured at each site. Standard errors of the mean are shown in parentheses.

Site Number	Number of Shrubs Measured	Density (individuals/m^2)	Mean Canopy Volume (m^3)	Median Canopy Volume (m^3)	Interquartile Range of Canopy Volume (m^3)
1	235	0.083	1.609 (0.293)	0.0007	0.076
2	145	0.051	2.01 (0.327)	0.814	1.986
3	418	0.148	0.48 (0.053)	0.0457	0.4127
4	337	0.119	0.261 (0.023)	0.1759	0.2471
5	144	0.051	1.992 (0.358)	0.407	2.223
6	160	0.057	0.65 (0.098)	0.4418	1.0505
mean	230	0.081	1.14	0.315	1.00

Table 4. Results of a two-way ANOVA of saltbush (*Atriplex polycarpa*) midday branchlet water potentials between six sites (n = 9/ site) and two seasons in the Comanche Point region of Tejon Ranch in the San Joaquin Valley of California. Measurements were taken on clear, sunny days in the winter (February 21) and fall (October 4) of 2017.

Source of Variation	df	SS	MS	*F*	*P*
Site	5	60.20	12.040	58.10	0.000
Season	1	434.52	434.524	2096.63	0.000
Site*Season	5	65.96	13.191	63.65	0.000
Error	96	19.90	0.207		
Total	107	580.58			

Table 5. General edaphic characteristics, bulk mineral assemblages, and clay mineral assemblages of six saltbush (*Atriplex polycarpa*) sites in the Comanche Point region of Tejon Ranch in the San Joaquin Valley of California. Edaphic Characteristics are from three homogenized 10 cm soil cores per site, taken in October 2017. Bulk and clay mineral samples were taken and run in June 2017.

Site Number	1	2	3	4	5	6
			General Edaphic Characteristics			
Soil Texture	Sandy clay loam	Loamy sand	Sandy loam	Sandy clay loam	Sandy loam	Sandy loam
Soil pH	7.1	7.4	7.3	7.6	7.7	7.9
Salinity- ECe dS/m	1.00	0.79	7.36	14.5	1.47	1.41
Available P mg/kg	11.2	10.7	12.7	21	13.2	24
Available K mg/kg	510	290	432	374	494	839
Available N mg/kg	6.24	2.33	2.95	16.1	6.67	4.81
Available Zn mg/kg	0.52	0.72	0.38	0.97	1.28	0.98
Available Fe mg/kg	6.85	8.37	4.46	3.30	7.00	5.25
Available Cu mg/kg	0.44	0.49	0.43	0.63	0.47	0.40
Available Mn mg/kg	9.33	9.36	19.7	13.8	13.5	18.7
Available S mg/kg	7.2	7.6	315	456	21.4	11.1
Organic Matter %	1.6	1.1	1.2	1.6	2.1	1.8
			Bulk Mineral Assemblages			
Clays %	1.10	7.31	0.53	1.52	0.43	0.36
Gypsum %	78.0	0	0	66.37	0	0
Plagioclase %	21.1	0	0	32.11	0	0
Amphiboles %	0	0	3.7	0	0	4.63
Quartz %	0	29.2	39.43	0	50.0	21.8
Ilmenite %	0	13.3	8.14	0	0	0
Albite %	0	50.2	48.3	0	49.7	34.4
Cristobalite %	0	0	0	0	0	19.4
Witherite %	0	0	0	0	0	19.43
			Clay Mineral Assemblages			
Smectite %	90.0	42.4	15.5	37.1	85.64	91.5
Illite %	3.7	42.4	53.3	32.41	8.12	0
Chlorite/ kaolinite %	6.3	6.41	31.21	31.0	6.24	8.5

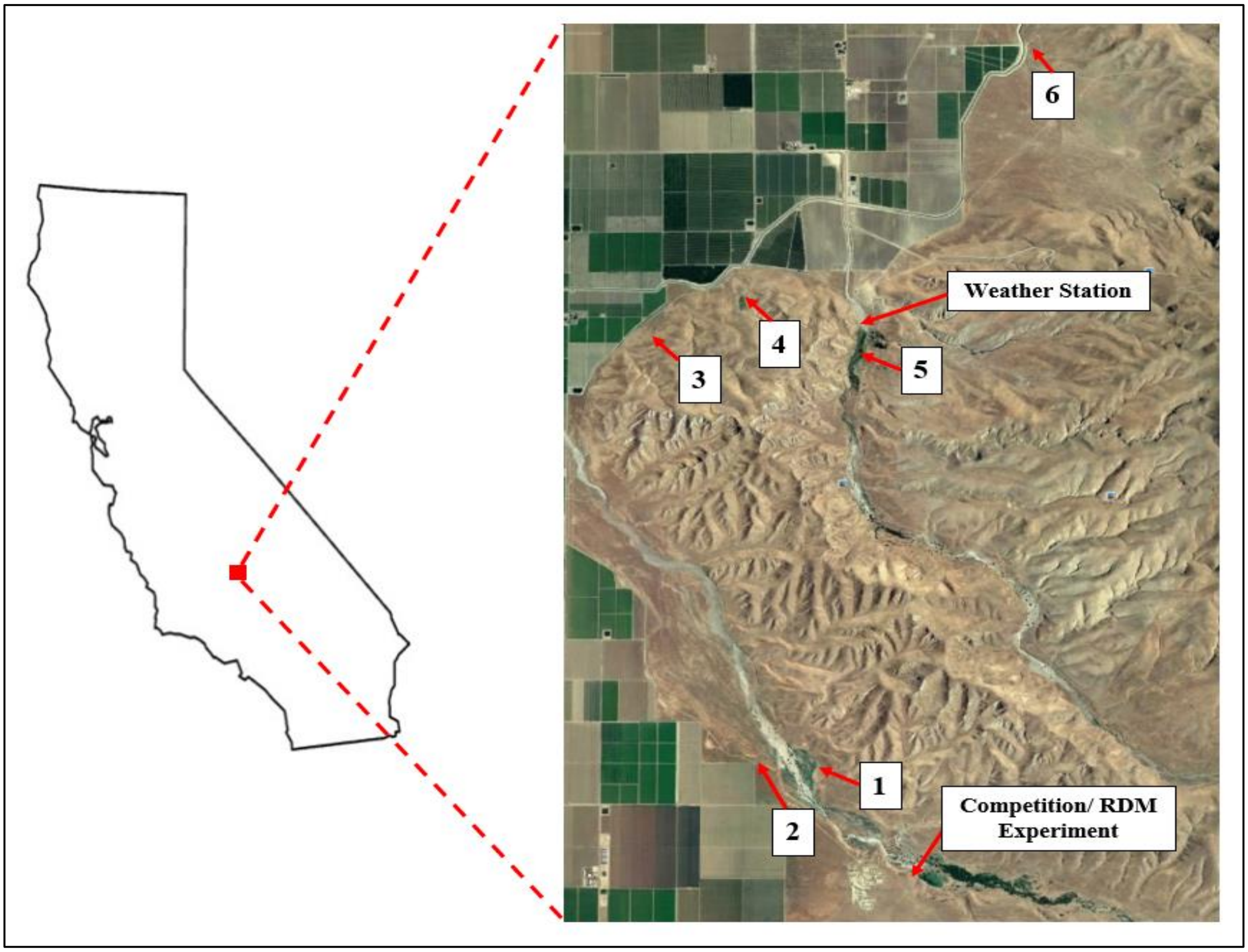

Figure 1. Location of six study sites around the Comanche Point region of Tejon Ranch in the San Joaquin Valley of California. Sites 1-6 are isolated remnant stands of the saltbush *Atriplex polycarpa*. The invasive grass competition and residual dry matter (RDM) experiment was conducted in an exclosure area to ensure no disturbance from cattle. Data from the weather station was used to generalize environmental context across all six sites. Aerial image from Google Earth.

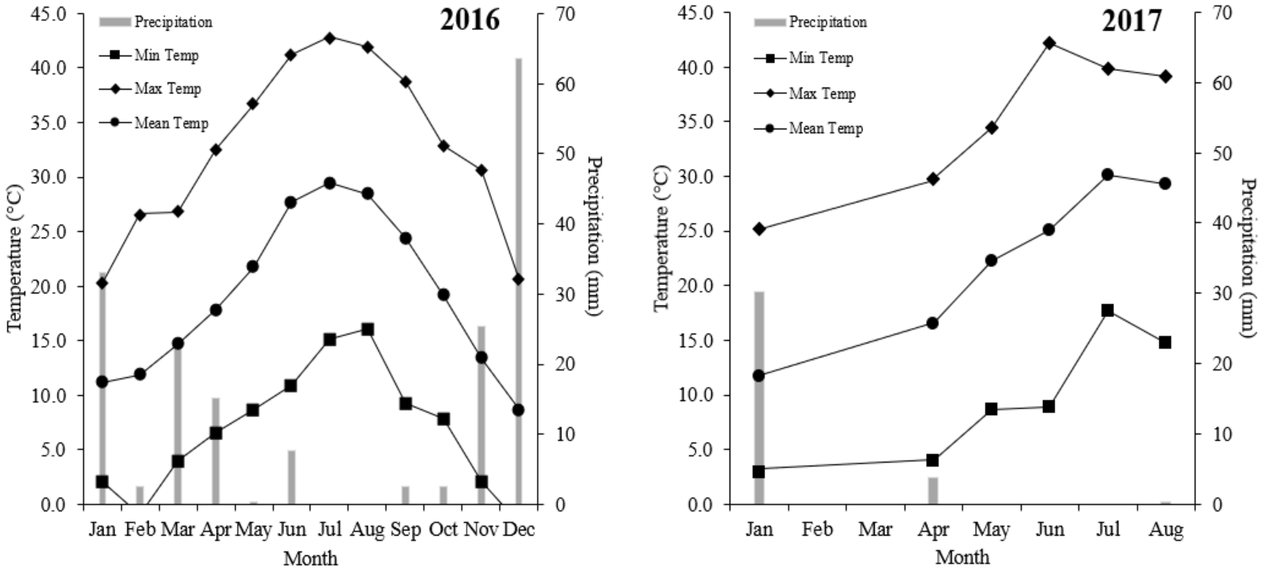

Figure 2. Mean, max, and minimum air temperatures and total precipitation by month in 2016 and 2017 from the weather station in the Comanche Point region of Tejon Ranch in the San Joaquin Valley of California. Data from 2017 was available up to August. February and March data in 2017 were unavailable.

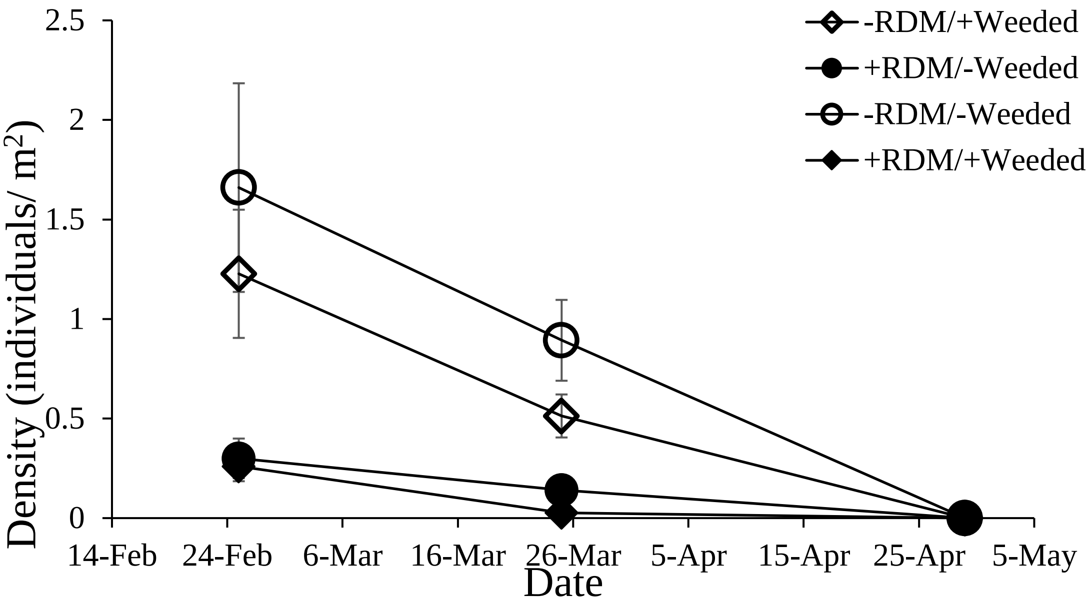

Figure 3. Seed sowing experiment showing mean density of saltbush (*Atriplex polycarpa*) seedlings by treatment between February and April 2017 at Tejon Ranch in the San Joaquin Valley of California. Plots were variably weeded or unweeded of invasive annual grasses and treated or untreated with a standard amount of residual dry matter (RDM) to assess the grass-related effects on saltbush germination and rate of mortality. Symbols means and errors bars are 95% confidence intervals.

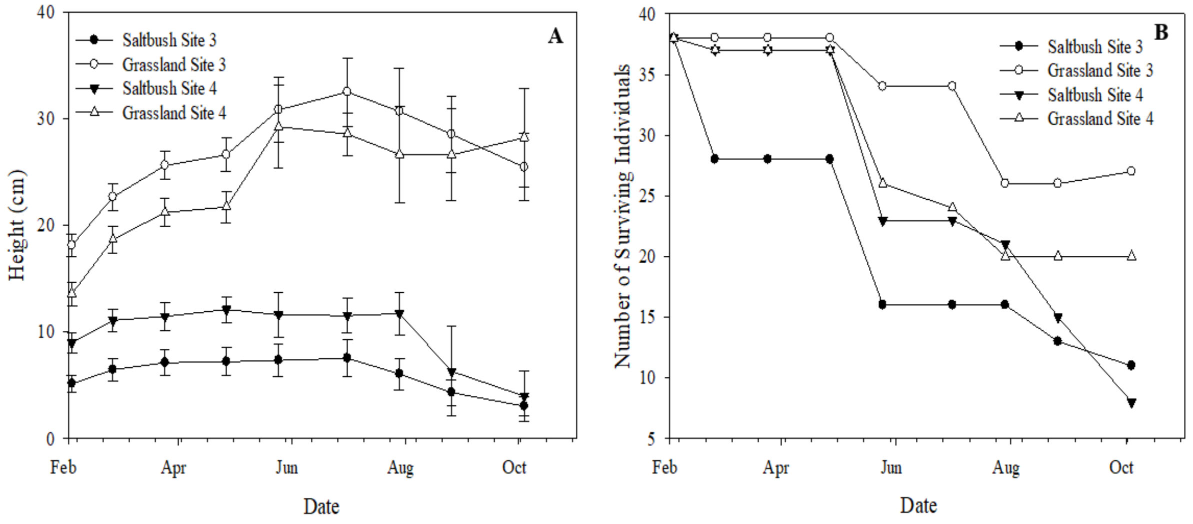

Figure 4. A) Mean heights and B) the number of surviving transplanted saltbush (*Atriplex polycarpa*) seedlings between February and October 2017, at two sites in the Comanche Point region of Tejon Ranch in the San Joaquin Valley of California. At each site, half of the seedlings (n =38) were planted in native saltbush habitat, while the other half were planted in adjacent invasive annual grassland. Seedlings were planted in late January 2017. Symbols means and error bars in panel A show standard errors of the mean.

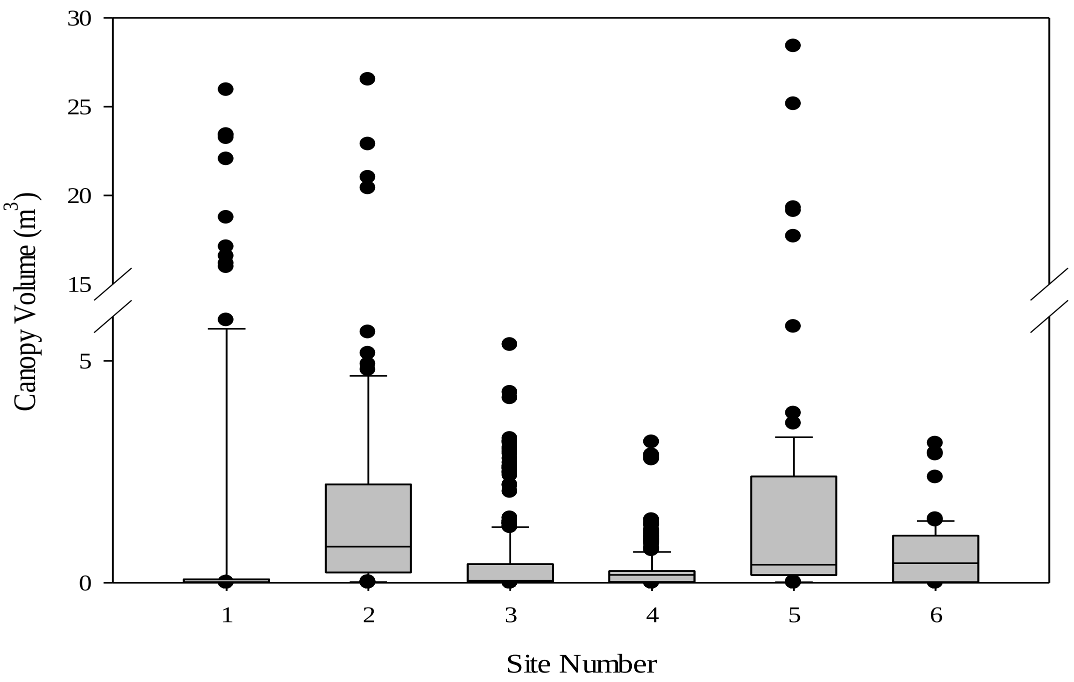

Figure 5. **S**ix saltbush (*Atriplex polycarpa*) sites at Tejon Ranch between Many and December 2016. The boxes show median (middle line) and interquartile ranges (top and bottom lines) of canopy volumes of shrubs at each site. Black dots represent outliers: shrubs which are substantially larger than most of the other shrubs by site. Shrub size estimates demographic composition by site.

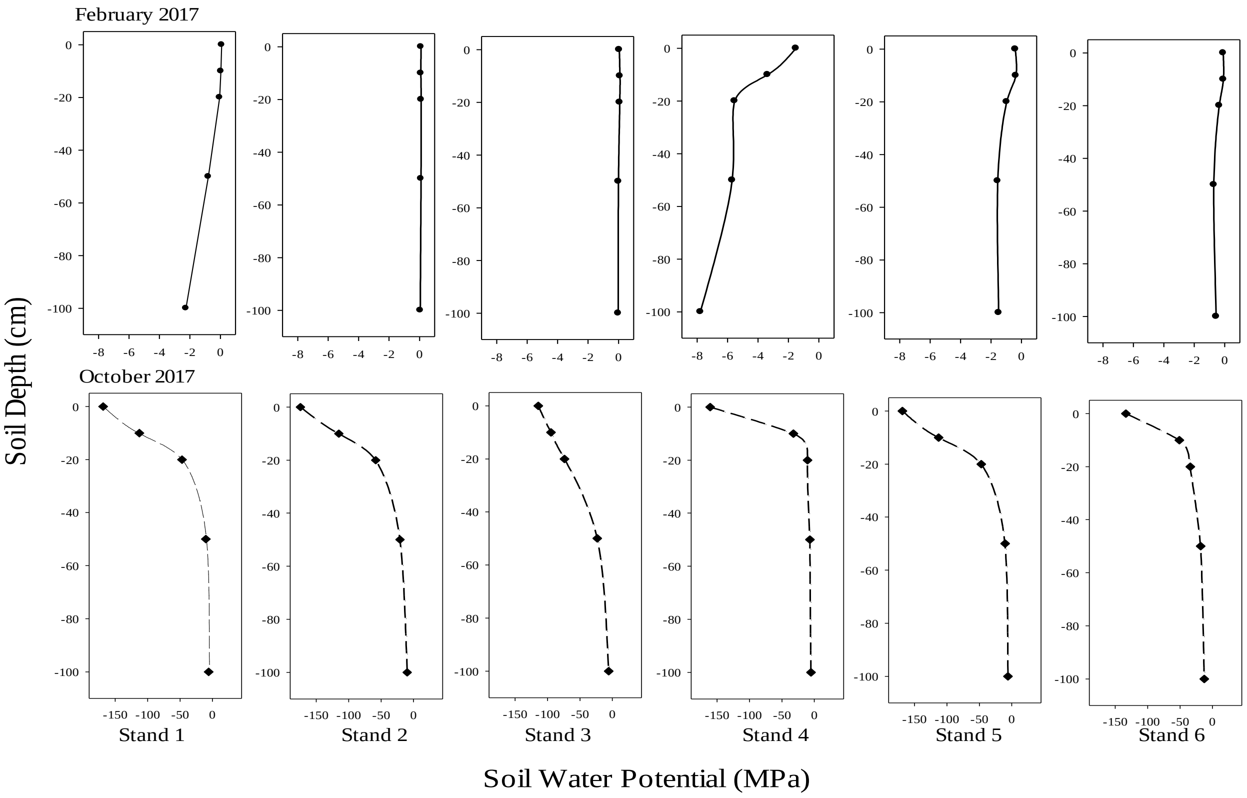

Figure 6. Soil water potential values at various depths amount six saltbush (*Atriplex polycarpa*) stands in the Comanche Point region of Tejon Ranch in the San Joaquin Valley of California. One sample was measured per site, per depth, per season. The top row (circles, solid line) shows water potentials in the winter of 2017 (February 21). The bottom row (diamonds, dashed line) shows water potentials in the fall of 2017 (October 4).

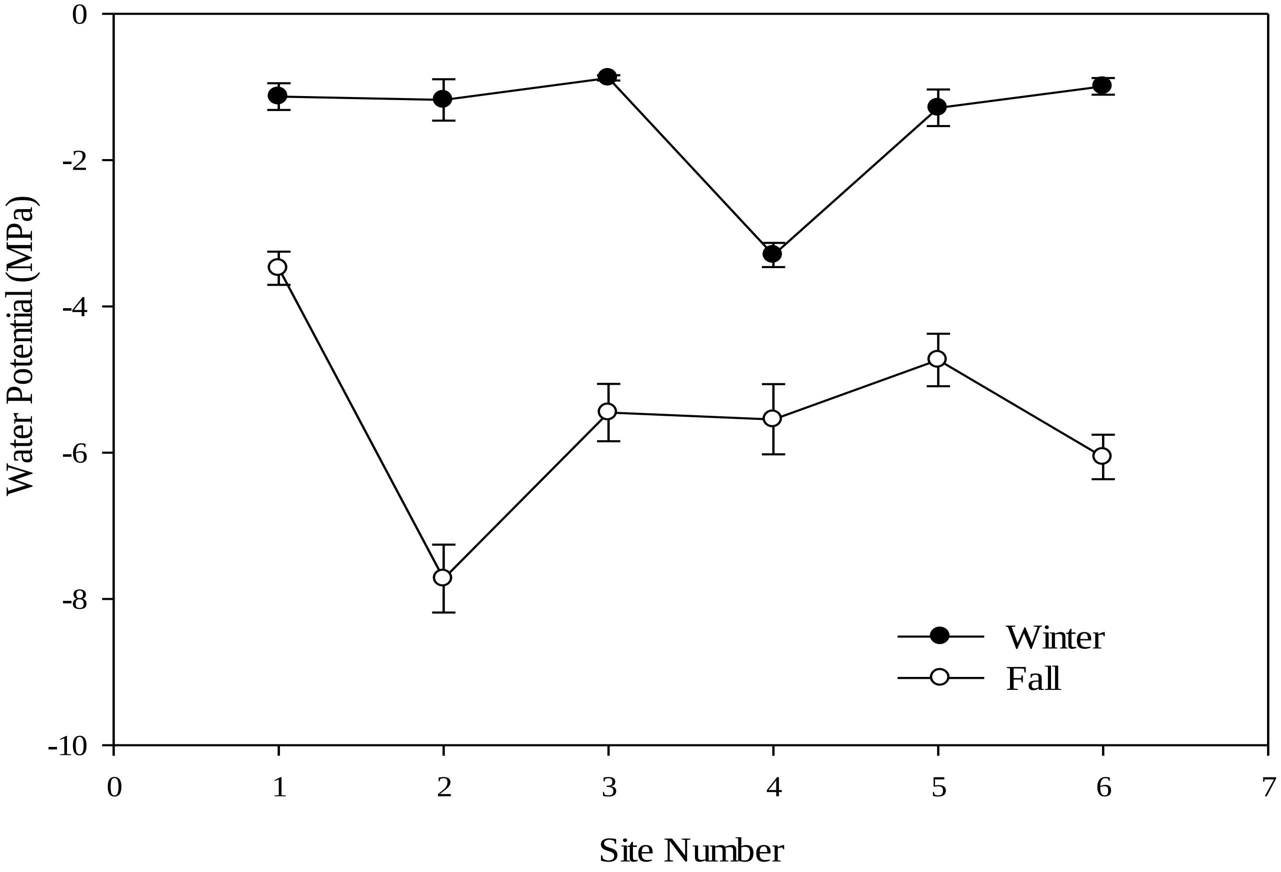

Figure 7. Mean (n= 9) midday branchlet water potentials of saltbush shrubs (*Atriplex polycarpa*) at six sites located in the Comanche Point region of Tejon Ranch in the San Joaquin Valley of California. Measurements were taken on clear, sunny days in the winter (February 21) and Fall (October 4) of 2017. Symbols are means, and error bars are standard errors of the mean.

Chapter 4

Conclusions

Saltbush recruitment is hampered by invasive annual grasses in the San Joaquin Valley (SJV). The grasses primarily inhibit saltbush germination and lead to greater levels of mortality of germinated seedlings. Key in limiting germination was the residual dry matter (RDM) left over from the previous years. Temperature, moisture, and light levels are altered due to the presence of invasive grasses and these changes impact germination, though the degree to which each plays a role and any interactions remains unclear. Alteration of surface soil temperatures at the time of germination in February or March is likely a key factor in limiting germination.

It also appears that periodic droughts in the last 200 y have repeatedly decreased the competitiveness and RDM production of the grasses and enabled concurrent saltbush recruitment events. Such events also likely lead to elevated saltbush mortality due to direct effects of drought and increased browse pressure. If saltbush stands are not expanding throughout the SJV, as I have observed at some sites, then mortality is equal to or greater than recruitment. These recruitment events are also observable in some mature Valley Saltbush Shrubland (VSS) stands as they contain a mix of ages rather than a more even age structure. However, demographic structure of the shrubs is more uniform in some saltbush stands suggesting local site differences may be important. Different saltbush sites have variable rates of recruitment, including both germination and survival of saltbush seedlings. One potentially important factor controlling variable recruitment rates, aside from light, temperature, and moisture, is soil composition. Soil composition across the various saltbush sites at Tejon Ranch differed and saltbush can occur on a variety of soil types with different availabilities of nutrients necessary for plant growth.

Saltbush seedlings can perform better amid annual grasses compared to those seedlings growing in native saltbush habitat. This is largely due to the pressures of higher herbivory from small mammals in native saltbush habitat. The likely herbivores were rabbits based on herbivory patterns, but this should be verified with direct observations. This finding is important because it suggests that saltbush seeds and seedlings are in conflicted in the context of recruitment. Saltbush seeds germinate optimally in open, sunny conditions free from invasive grass competition and RDM. In contrast, seeds which successfully germinate and survive the first few months of life in grassy areas end up surviving longer because of reduced pressures of herbivory.

Other studies have found similar seed-seedling conflicts (Lamont et al. 1993, Schupp 1995). This finding presents potentially important consequences for attempts at restoring saltbush in the SJV. Clearing away of grasses, specifically RDM, is an important management tactic. Thus, a simple management tactic of clearing away of RDM and seeding with saltbush seeds can prove effective (Fig. 1). This has been implemented at Windwolves Preserve to good effect. In some cases where herbivory is high then exclosures may prove additionally useful, but as Fig. 1 shows, there are abundant seedlings of saltbush recruiting outside of the protected area.

Figure 1. Mammal exclosure around *Atriplex polycarpa* seedlings at the Wind Wolves Preserve, in the San Joaquin Valley of California. Management tactics involving clearing away invasive grass residual dry matter and seeding with saltbush seeds is effective in promoting saltbush recruitment. In many cases animal exclosures may not be needed as shown in the figure where many saltbush seedlings are establishing outside of the protected area.

Another important consideration is that saltbush communities occur globally throughout arid and semi-arid regions, but most are not as heavily degraded as communities in the SJV and do not experience the pressures of elevated rates of species invasion and N deposition. *Atriplex polycarpa* specifically thrives as a common Mojave Desert shrub, east of the SJV. However, disturbance, climate change, and N deposition can lead to increased grass invasions in the deserts (Dukes and Mooney 1999). This study contributes to understanding future expected transformations that might affect deserts, but these conditions are already apparent in the SJV due to the different climatic conditions and environmental changes in the last 200 y.

Saltbush shrublands can be considered model communities to study the effects of climate change on plant communities in the Anthropocene because arid shrublands are predicted to become more prevalent with changing climatic patterns, and many saltbushes thrive in conditions of disturbance (Chatterton 1971, Sankary and Barbour 1972, Mikhiel et al. 1991, Lenihan et al. 2003). With global changes in precipitation and temperature, some areas are likely to become drier and more saline, conditions ideal for saltbush recruitment. The ecological niche of saltbush shrublands may become more abundant worldwide; thus, understanding the factors affecting saltbush recruitment and the associated ecological services are important ecological and management considerations.

Literature Cited

Chatterton, N. J., J. R. Goodin, C. M. Mckell, R. V. Parker, and J. M. Rible. 1971. Monthly variation in the chemical composition of desert saltbush. Journal of Range Management 24:37-40.

Dukes, J. S. and H. A. Mooney. 1999. Does global change increase the success of biological invaders? Tree 14:135-139.

Fenn, M. E., J. S. Baron, E. B. Allen, H. M. Rueth, K. R. Nydick, L. Geiser, W. D. Bowman, J. O. Sickman, T. Meixner, D. W. Johsnon, and P. Neitlich. 2003. Effects of nitrogen deposition in the western United States. Bioscience 53:404-420.

Germano, D. J., G. B. Rathburn, and L. R. Saslaw. 2001. Managing exotic grasses and conserving declining species. Wildlife Society Bulletin 29:551-559.

Lamont, B. B., Witowski, E. T., and N. J. Enright. 1993. Post-fire litter microsites: safe for seeds, unsafe for seedlings. Ecology 74:501-521.

Lenihan, J. M., Drapek, R., Bachelet, D., and R. P. Neilson. Climate change effects on vegetation distribution, carbon, and fire in California. Ecological Applications 13:1667-1681.

Mikhiel, G. S., S. E. Meyer, and R. L. Pendleton. 1992. Variation in germination response to temperature and salinity in shrubby *Atriplex* species. Journal of Arid Environments 22:39-49.

Sankary, M. N., and M. G. Barbour. 1972. Autecology of *Atriplex polycarpa* from California. Ecology 53:1155-1162.

Schupp, E.W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 10:399-409.