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Relationships of exotic plant invasions with biological soil crust, desert pavement, and soil carbon in the eastern Mojave Desert

Adria DeCorte
University of Nevada, Las Vegas

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RELATIONSHIPS OF EXOTIC PLANT INVASIONS WITH BIOLOGICAL SOIL CRUST, DESERT PAVEMENT, AND SOIL CARBON IN THE EASTERN MOJAVE DESERT

by

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ABSTRACT

Relationships of Exotic Plant Invasions with Biological Soil Crust, Desert Pavement, and Soil Carbon in the Eastern Mojave Desert

by

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In a matter of 50 years, exotic annual plants have become widespread in the Mojave Desert, contributing to drastic landscape changes such as those caused by recent fires. Invasions by exotics threaten native Mojave Desert plant communities by altering community functions (e.g. fire regimes) and by reducing plant diversity. Because it is not practical, or even possible, to eradicate these exotics, developing effective prevention techniques is the key to controlling these invasions.

This thesis used a greenhouse experiment, a field experiment, and a correlational field study to examine the affect soil surface types have on the establishment of three exotic plant species in the Lake Mead National Recreation Area of the eastern Mojave Desert. The species studied were Bromus rubens, Schismus spp., and Brassica tournefortii, and the soil surface types were biological soil crust, desert pavement, and areas free of rock mantle and living crust that are referred to as “open.” Also examined were the effects that carbon addition and disturbance have on the establishment of these species.

The results, analyzed using analysis of variance models, showed a correlation between carbon addition and the reduction of density and biomass in all three exotic species studied. In the field experiment, Bromus had a 69% reduction in density and a
93% reduction in biomass when carbon was added to the soil, and *Schismus* had an almost 100% reduction in density and biomass with carbon addition. In the greenhouse, carbon addition almost entirely eliminated Brassica germination, and Schismus density decreased by 49% on open surfaces and 65% on crust.

Disturbance by hand-raking had no significant effect on establishment, and establishment varied by surface type with mixed results. At the field experiment site, where establishment on biological soil crust was compared to that on desert pavement, there was 83% more Bromus on crust than on pavement, but Schismus showed no significant correlation with surface type. In the greenhouse, where establishment on crust and pavement was compared to that on open surface, there was higher overall establishment on open surfaces. Schismus had the strongest response, with 63% higher density on open than crust and 87% higher density on open than pavement. Brassica had 36% higher density on open than crust or pavement.

When plant community data from the correlational field study were analyzed using analysis of variance models, plant cover was higher on open sites than biological soil crusts and higher on crusts than pavement. Both open sites and crusts had higher species diversity than pavement. Multivariate community analyses showed that there were significant differences in annual plant community composition on crust at each of the sites surveyed. On the field experiment treatment plots, there was a significant difference between community composition for interactions between surface type and carbon addition and between surface type and disturbance.

Protection of biological soil crust and desert pavement in conjunction with carbon addition could serve as useful tools for limiting the spread of invasive species in the
Mojave Desert. These two surface types, pavement especially, exhibited lower exotic establishment than that on open surfaces. Using carbon addition to reduce soil fertility was overall successful at reducing invasive plant establishment. Disturbance results contradicted the literature’s suggestions that disturbance is correlated with exotic establishment, a possible result of the short duration of the study.

These findings are expected to contribute novel information to the broader understanding of these factors in arid lands as well as to provide information applicable for local land managers tasked with protecting desert soil surfaces and minimizing the impacts of exotic species.
ACKNOWLEDGEMENTS

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Without the assistance with fieldwork and encouragement that my husband Jarrett provided me, the study would have been difficult to complete. Cayenne Engel also provided essential insight and feedback during the entire process and was a tremendous resource throughout. Statistician Cheryl Vanier was instrumental in performing ANOVA analyses for the three components of my study. Botanists Sarah Schmid and Karin Edwards helped with the annual plant survey, and Nevada Conservation Corps members aided in the soil salvages.

This research was supported through a cooperative agreement between the National Park Service (Lake Mead National Recreation Area (LMNRA)) and the University of Nevada, Las Vegas, coordinated by Alice Newton and Kent Turner of LMNRA. I thank LMNRA for permitting my study within their borders, and the LMNRA Nursery staff, especially Janis Lee, for watering and the use of their greenhouse.
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CHAPTER 1

INTRODUCTION

The goal of this research was to contribute ecological information that aids in limiting the spread of invasive plant species in the eastern Mojave Desert. Since the mid-20th century, three annual plant species (Bromus rubens, Schismus sp., and Brassica tournefortii) of Mediterranean origin have been spreading through low desert areas of the southwestern United States (Bossard et al. 2000). They have proved to be a threat to local native plant communities by altering community functions (e.g. fire regimes) and by dominating the annual biomass of plant communities. As a result, fire cycles destroy long-lived woody species that are not evolutionarily adapted to recover from fire, and late-successional native plant diversity is reduced (Bossard et al. 2000; Cook et al. 2007).

Ecological restoration in the Mojave Desert seeks to mitigate the effects of these invasions while limiting the further spread of exotic species. Possible exotic species-control techniques include manual pulling, mechanically mowing, encouraging competition from natives, grazing, biological controls, herbicides, prescribed burns, and solarization, a technique where weed seeds in the soil seedbank are killed by placing a plastic sheet over moist soil for at least a month (Bossard et al. 2000). The three exotics studied here are all well-established in the system, so eradication is not a practical solution. Research into the best methods for controlling invasions within the Mojave Desert is currently ongoing, but it is generally agreed that preventing the spread of exotics is the best means of control (Bossard et al. 2000).

Explored in this thesis are tools for limiting further invasions by targeting two key factors tied to invasibility: nutrient availability and disturbance. The reduction of soil
nitrogen availability following carbon-addition has been shown to reduce invasive species in other ecosystems (Morgan 1994; Reever Morghan and Seastedt 1999; Alpert and Maron 2000; Paschke et al. 2000), and demonstrating its applicability to desert ecosystems could provide an excellent management tool for controlling further invasions. It is also possible that natural soil surfaces such as biological soil crust and desert pavement reduce the establishment of invasive species. Desert pavement does, in fact, correlate with lowered plant establishment (Shreve 1951). Studies on crust have been more contradictory, but it is possible that a species-specific response pattern could inhibit invasives (Serpe et al. 2006; Serpe et al. 2008; Belnap et al. 2001). Disturbance has been linked to community invasibility (Davis et al. 2000), and protecting these soil surfaces could be a key factor in reducing the spread of invasives.

All research in this thesis was performed on low-elevation (300-800 m) *Larrea-Ambrosia* communities within Lake Mead National Recreation Area, an area which is invaded by the study species and is also representative of eastern Mojave Desert wildlands. The general objectives of this research were to: (i) determine whether biological soil crust or desert pavement inhibit the establishment of the three target invasive species, (ii) evaluate the effectiveness of carbon addition as an invasive species treatment technique in desert ecosystems, (iii) determine the effects of disturbance on these target invasives, and (iv) develop management techniques for land managers within desert ecosystems. The study pertaining to each of these objectives is presented in a manuscript chapter following a literature review chapter. The literature review compiles known information on invasibility, biological soil crust, desert pavement, disturbance, and carbon addition and their relationships to each other, including the findings of past
related studies. The thesis concludes with a chapter synthesizing major conclusions of this research and identifies topics for future research. My emphasis in this thesis is on increasing the understanding of invasive species interactions within the Mojave Desert and on suggesting how results relate to applied desert ecological restoration.

Literature Cited


CHAPTER 2
LITERATURE REVIEW

Introduction

Ecologists in the deserts of the southwestern United States are faced with the challenge of developing strategies for limiting the future spread of invasive plants. Due to a globalized trade system and ever-expanding urbanization, invasive plant species are on the rise worldwide. To date, there have been few studies published on invasive species management within arid ecosystems. Reliable techniques for controlling invasive annual plants in deserts are not well developed, and there is a great need for more information on this matter.

Invasion has been linked to plant community stress; when a community is disturbed or otherwise compromised, exotics are more likely to invade (Brooks 1998). While management techniques proposed for hot deserts such as the Mojave include herbicide, it may be more useful to focus on managing the community by techniques such as adding native vegetation that can compete with exotics (Allen et al. 2005). Furthermore, increasing the health of the native plant community in order to fortify it against invasion may prove to be the most effective control method. This includes protecting the soil and plants from disturbance and may include lowering nutrient availability to levels that only natives can utilize effectively (Brooks 1998). Native desert plants thrive under low-nutrient conditions, while local invasive exotics are from more fertile areas. Consequently, effective techniques might include lowering soil fertility to levels best utilized by natives and not exotics. Once invasive species are established and
widespread, eradication is expensive (Brooks and Pyke 2001), but costs can be reduced by limiting further invasions through strengthening native plant communities.

Plant Community Invasibility

If left alone, invasive plant species have the potential to damage entire ecosystems. Instead of incorporating into ecosystems, invasive species often dismantle and destroy ecosystem functions (D’Antonio and Vitousek 1992). Worldwide, they are one of the greatest threats to biodiversity (Wilcove et al. 1998), and almost half of the threatened and endangered species in the United States owe their status to invasive exotic species (Pimentel et al. 2004). When resource managers from 35 protected areas within Nevada and Arizona were surveyed, about half of them said that exotic plants were threats to rare plant populations within their areas (Springer et al. 2010).

As the global population expands, more opportunities for invasion are created. Mojave Desert cities such as Las Vegas, Nevada, and Victorville, California, have doubled their population in the last decade and continue to grow (US Census Bureau 2010). Because plant invasions are facilitated by roads and the spread of cities (Starr and Mefford 2002), this population boom has coincided with an increase in invasions (Bossard et al. 2000). Expanding cities are also responsible for increased habitat destruction which weakens native plant communities and provides new opportunities for invasive species to infiltrate (Starr and Mefford 2002). Human facilitation means that invasives can travel farther and faster than ever before. Creosote bush (Larrea tridentata), one of the Mojave Desert’s dominant shrubs, took thousands of years to invade and establish itself in North America (Wells and Hunziker 1976). Now, invasive
plant species can establish within a mere moment of evolutionary time (D’Antonio and Vitousek 1992; Bossard et al. 2000).

Invasive species are not just an ecological issue; they negatively impact the economic sector as well. In the U.S., it is estimated that over $120 billion in agriculture and ecosystem services is lost annually due to invasive species (Pimentel et al. 2004). In addition, invasive species often compromise the aesthetic value of ecosystems, affecting tourism. In the deserts of southwestern U.S., the loss of iconic species like the Joshua tree (*Yucca brevifolia*) and saguaro cactus (*Carnegiea gigantea*) can change the entire visual landscape. They draw visitors and are, themselves, an integral part of the tourism industry (Narong et al. 1995). Las Vegas attracts over 35 million visitors every year, and the Las Vegas Chamber of Commerce (2010) promotes tourism at nearby natural areas like Red Rock National Conservation Area. People who come to see the pristine beauty of this natural Mojave Desert ecosystem are now met with vast areas of burn scars and fields of invasive grass.

Ecosystem harm caused by invasive species can make more work for agencies. For example, in the Mojave Desert, the Endangered Species Act requires agencies to manage the land with the goal of protecting the desert tortoise (Esque et al. 2003). Recent fires caused by invasive grasses have resulted in burned woody shrubs, reducing thermal and predation cover for tortoises. In addition, due to their slow movement, tortoises are killed during the ensuing fires. Consequently, controlling the spread of exotic grasses would simplify desert tortoise management (Esque et al. 2003).

One of the greatest threats to the Mojave Desert is this new fire regime created by the invasion of red brome (*Bromus rubens*) and Mediterranean grass (*Schismus* spp.),
both exotic annual grasses of Mediterranean origin. *Schismus* spreads into the interspaces between shrubs, an area that was historically open, and the highly flammable *Bromus* colonizes the fertile islands underneath shrubs, resulting in a hotter, killing fire that destroys the shrub (Bossard et al. 2000). In addition to providing a high fuel load of dry brush when they die in the summer, these grasses connect fertile islands, allowing for the quick spread of fire. In 2005, a total of 3% (over 385,000 hectares) of the entire Mojave Desert burned (Brooks and Matchett 2006).

Before the invasion of these exotic species, fires were rare in the Mojave Desert, and, consequently, the native flora is not evolutionarily adapted to recover from fire (Brooks 2002). In contrast, Mediterranean-origin grasses evolved with regular fire in their native regions (Naveh 1975). This results in the rebound of exotic grasses following a fire (D’Antonio and Vitousek 1992) and slow, if at all, recovery of native vegetation, especially woody species such as Joshua trees (*Yucca brevifolia*) and blackbrush (*Coleogyne ramosissima*) (Abella et al. 2009). These fires frequently alter plant community structure, replacing woody perennial scrub with exotic annual grassland, dominated by *Bromus* and other exotics (Brooks 2000a). Although older *Yucca brevifolia* can resprout following fire, recruitment from seed and the resprouting of smaller plants is minimal, and this threatens the future of this species and the plant communities it is associated with (DeFalco et al. 2010).

Furthermore, global climate change is predicted to have some of its greatest effects on arid ecosystems. In Mojave Desert experiments using free-air CO$_2$ enrichment technology, it was found that when CO$_2$ levels increased, it resulted in a greater increase in the above-ground biomass and seed production of *Bromus rubens* than several species
of native annuals exhibited (Smith et al. 2000). This leads to a greater probability of *Bromus* dominance in native plant communities, a factor which could significantly alter plant community composition and result in an ever greater fire frequency (Smith et al. 2000). Increasing nitrogen deposition, another result of climate change, will result in higher soil fertility (Sala et al. 2000), which may favor invasive species that originated in more fertile environments.

The Mojave Desert is typically characterized by low exotic species richness and high exotic annual species dominance, meaning that just a few invasive exotics have become dominant (Brooks 1998). Three of these dominant invasive species in the eastern Mojave Desert are *Bromus rubens*, *Schismus* spp., and *Brassica tournefortii*, winter annuals that originated in the more fertile Mediterranean region (Bossard et al. 2000). Although all three of these species were present previously, they became widespread and problematic in the southwestern deserts of the US during the mid-20th century (Bossard et al. 2000), coinciding with the spread of humans in this area. All three of these species have the tendency to dominate the biomass of the plant communities they invade, becoming fire hazards when they die back in the spring. These species have infiltrated plant communities so completely that eradication is impossible. The solution lies, instead, in controlling current populations and mitigating the future spread of these species into virgin habitat. For these three species, most common control techniques would be either ineffective or impractical at large scales. Using techniques such as grazing, prescribed burning, and mechanical removal for these species would be counterproductive because these techniques would disturb the land, further facilitating the establishment of these species (Bossard et al. 2000). Herbicide can be used for
smaller populations, but is impractical on a large scale, and there is concern for the effects it has on non-target organisms such as native plants (Bossard et al. 2000). It is possible that invaded desert areas could be inoculated with a black smut species, *Ustilago aegyptica*, that attacks *Schismus*, causing massive damage to flowering structures, but more research is needed into this method (Brooks 2000b).

*Bromus* is most common on lands disturbed by wildfire, grazing, off-road vehicles, or agriculture (Newman 1992). The disturbances that most influence *Bromus* invasion potential are grazing and fire because they clear vegetation from the surface, removing competition which allows *Bromus* to quickly dominate the plant community (Newman 1992). Repeated disturbances, such as recurring fires, favor establishment (Beatley 1966). *Bromus* establishment is limited by water and resources in desert regions (Brooks 2000a). Populations increase during years of average or higher rainfall and seedling mortality is high during years of low rainfall, depleting the seedbank (Brooks 2000a). Consequently, *Bromus* tends to grow in microhabitats such as fertile islands beneath shrubs (Beatley 1966).

*Bromus* invasion potential is high. Because germination is stimulated by only one centimeter of rainfall, compared to the two and a half centimeters required by natives, *Bromus* germinates earlier than natives, allowing the exotic grass to partition resources ahead of natives (Hammouda and Bakr 1969). In the wild, it produces 76 seeds per plant, and a square meter of dense *Bromus* can produce over 83,000 seeds (Wu and Jain 1979). Seed is easily dispersed long distances by attaching itself to clothing and animal fur and over short distances by wind (Brooks 2000a).
Due to its key role in recent Mojave Desert fires, it is urgent that control measures for the spread of *Bromus* be developed. Following a few years of drought, small populations of *Bromus* have been eliminated, and it is believed that this species is short-lived (2-3 years) in the seedbank (Brooks 2000a). On small, isolated sites that lack seed-rain from nearby sites, manually pulling *Bromus* plants prior to reproductive maturity could potentially eliminate *Bromus* populations. Theoretically, if an area was eradicated of the species and new introductions were prevented, within a few years, it could be *Bromus*-free (Brooks 2000a).

The annual grass species *Schismus barbatus* and *S. arabicus* are genetically and morphologically similar (Faruqui and Quarish 1979), and are referred to in this thesis collectively as *Schismus* spp. Because *Schismus* evolved in the more arid regions around the Mediterranean, it does not tolerate shading well (Brooks 1998) and establishes in interspaces between shrubs (Brooks 2000b). This species is somewhat limited by water; in the wild, water stress ends the plant’s life cycle (Brooks 2000b). In greenhouse conditions, it can grow, spread, and reproduce for up to two years if irrigation continues (Gutterman 1989).

*Schismus* proves to be a strong competitor against native annual species which historically occupied the interspaces between shrubs (Brooks 1998). Since the introduction of *Schismus*, the native annual grass *Vulpia octoflora* has become more infrequent (Brooks and Pyke 2001). *Schismus* competes with native annuals for limiting nutrients; studies have shown that it uses more soil nitrogen at a faster rate than natives do, inhibiting natives’ growth rates (Brooks 1998). In addition, presence of *Schismus* results in lower native seedling biomass (Brooks 2000c).
This species often forms a carpet of grass in interspaces between shrubs (Brooks 2000b), and when it dries up upon senescence, the dead material provides fire fuel which connects fertile islands via those interspaces (Brooks 1998), contributing to the recent increased fire frequency in the Mojave Desert. *Schismus* invasion potential is high, as it has been shown to respond positively both to water and disturbance, key factors believed to facilitate the spread of invasives (Suazo et al. 2009). *Schismus* often establishes in areas where shrub cover is reduced and soils are disturbed by grazing or off-highway vehicle use (Brooks 2000b).

*Schismus*’ dust-like seed is easily dispersed and is long-lived in the seedbank (James et al. 2006). During its growing season, *Schismus* seed production has been measured at greater than 1,000 seeds per m² plot of land per month (James et al. 2006). Like *Bromus*, *Schismus* can germinate on 1 cm of rainfall, and even less if it is in the right microclimate (Brooks 2000b). Its seed also exhibits other opportunistic germination strategies. Under optimal conditions, only 15% of the seedbank germinates at once (Gutterman 2003), ensuring persistence of the seedbank. Seeds are also influenced by post-maturation temperatures so that different seed lots may require different after-ripening processes, further diversifying the seedbank (Gutterman 2000).

*Brassica*, an invasive annual mustard, has become a management problem in areas such as the Lake Mead National Recreation Area (LMNRA) where it has spread into a wide range of habitats including open desert, beaches, and gravely washes (Bangle 2008). In *Brassica* removal experiments, it was found that the presence of *Brassica* reduces native plant reproduction, resulting in a community composition shift towards *Brassica* and a lower proportion of native species (Barrows et al. 2009). In addition, the
species’ seasonal abundance can suppress native wildflowers (Minnich and Sanders 2000) and interferes with native lizard and mammal behavior (Marshall et al. 2000).

Brassica has diverse mechanisms for establishment, increasing its threat to native species. For example, Brassica germinates earlier in the season than natives, survives for extended periods in the seedbank, can establish from the seedbank after a fire, and tolerates a wide range of temperatures during germination (Bangle 2008; Minnich and Sanders 2000). Studies have shown that Brassica germination is inhibited by light exposure, with an optimal depth for seed burial at 0.5cm (Thanos et al. 1991). Seeds laid on the soil surface experience total inhibition (Thanos et al. 1991). Brassica can flower as early as December and ends its life cycle in April to May (Minnich and Sanders 2000).

One Brassica plant can produce as much as 9,000 seeds which may live for several years in the soil (Minnich and Sanders 2000). When seedpods get wet, they become sticky, allowing them to latch onto animals and travel long distances (Minnich and Sanders 2000). Highways and washes are also corridors for the spread of seed, and, in open areas, the stem of the plant will break at ground level, allowing the plant to tumble along the ground, dispersing seed as it goes (Felger 1990). The survival of seed after extended submersion in water could lead to the introduction of Brassica on islands and isolated shoreline within LMNRA previously thought to be protected from invasion (Bangle 2008). Brassica seed has also been shown to germinate in soils that are moderately saline, raising the concern that this species may be able establish in areas already colonized by salt cedar (Tamarix spp.), an exotic invasive that has spread extensively throughout southwestern riparian areas (Bangle 2008). If Brassica could
establish within the monoculture that *Tamarix* creates by secreting salt into the soil, it would add a new dimension to the *Tamarix* control problem (Bangle 2008).

*Brassica* shows a boom-or-bust type of establishment; germinating en masse in years of higher than average rainfall and sparsely in years of lower rainfall (Barrows et al. 2009). Greater than four centimeters of precipitation in the fall to winter season can initiate mass germination of seeds in the seedbank (Minnich and Sanders 2000). This precipitation-related cycle makes it difficult to study *Brassica* control methods, as wet years are hard to predict and dry years often result in lower overall germination. Because *Brassica* is found most readily in disturbed sites like roadsides and abandoned fields, limiting disturbances from off-road vehicle use and construction activities would reduce potential habitat and result in a reduction in seed production. It is interesting to note that *Brassica* establishment is reduced by either intraspecific or interspecific competition when densities are high (Minnich and Sanders 2000). When *Brassica* density is high, its biomass decreases, and, in densely populated exotic grasslands (including those dominated by *Bromus*), *Brassica* establishment is suppressed (Minnich and Sanders 2000).

**Disturbance**

The term disturbance most often refers to the anthropogenic degradation of an ecosystem. Humans can directly cause a disturbance (e.g. off-road vehicle use) or they can indirectly cause a disturbance (e.g. through the introduction of wild horses and burros) (Lovich and Bainbridge 1999). Disturbance is widely recognized as playing an important role in facilitating invasions, possibly due to increased nutrient availability and decreased health of natives following a disturbance (Davis et al. 2000). Within the
Mojave Desert, *Bromus, Schismus*, and *Brassica* tend to occupy disturbed habitat (Newman 1992; Brooks 2000b; Minnich and Sanders 2000). In a study done within LMNRA, *Brassica* seed production was positively correlated with soil disturbance, suggesting a greater potential for population expansion and persistence after disturbance (Suazo et al. 2009). In this same study, *Schismus* sp. showed a positive response to both water and disturbance (Suazo et al. 2009). In contrast, while native annuals monitored in the study responded positively to increased water availability, they responded negatively under disturbed conditions (Suazo et al. 2009). This suggests that in disturbed areas, exotic annuals may outcompete and displace native annuals during reestablishment.

The desert recovers slowly from disturbances. After a large disturbance such as a fire or pre-development soil blading, it takes anywhere from decades to centuries for woody dominants such as *Larrea* and *Coleogyne* to reestablish their pre-disturbance abundance (Webb et al. 1987). Off-road vehicle tracks create compression and shear forces which have a strong effect on the soil, resulting in increased water runoff, faster erosion from wind and water, lower water infiltration, and less soil stabilizers (including biological soil crusts) (Eckert et al. 1979; Iverson et al. 1981; Webb 1982; Belnap and Gillette 1997).

From studies of historically dated disturbances such as ghost towns and military use, we know that compacted desert soils can take anywhere from 70-680 years to recover (Iverson et al. 1981; Webb et al. 1986, 1988; Prose and Wilshire 2000).

**Carbon Addition**

As climate change continues and atmospheric pollutants increase, nitrogen deposition is expected to also increase, resulting in elevated nitrogen levels in the soil (Brooks 2003). Due to lower maximal growth rates, plants native to low fertility
environments like deserts generally show less response to increased soil fertility than plants that evolved in more fertile environments (Chapin et al. 1986). Consequently, increased soil fertility leads to an increase in exotic species but minimal increase in natives. In a Mojave Desert study examining the effects of fertilization through nitrogen addition on exotic and native annuals, Brooks (2003) found that fertilization resulted in an increase in the density and biomass of exotic annuals *Bromus*, *Schismus*, and redstem strok’s bill (*Erodium cicutarium*). At the same time, density and biomass of native annuals decreased. Furthermore, native species richness decreased in the year of higher annual productivity, probably due to competition from exotic annuals. If the inverse is true and reducing soil fertility results in a decrease in exotic annuals while maintaining native populations, then lowering soil fertility may prove to be an important method for controlling Mediterranean-origin invasive species.

Techniques developed to decrease soil fertility by adding a carbon source have been somewhat successful for other ecosystems. Addition of carbon has been shown to decrease nitrogen levels in soil, resulting in lowered fertility (Reever Morghan and Seastedt 1999). The increase in C:N ratio is thought to stimulate soil microbes to immobilize nitrogen, resulting in lower nitrogen availability in the soil. In the handful of studies using carbon addition, it was shown to either limit the establishment of exotics or increase competitive ability of natives (Zink and Allen 1998; Morgan 1994; Reever Morghan and Seastedt 1999; Alpert and Maron 2000; Paschke et al. 2000).

Although the effects of carbon addition have been examined for prairies, coastal scrub, and wetlands (Morgan 1994; Reever Morghan and Seastedt 1999; Alpert and Maron 2000; Paschke et al. 2000), there is little to no documentation for arid regions.
When pine bark mulch was added for restoration purposes in disturbed coastal sage scrub habitat in California, the result was decreased soil nitrate, followed by a positive response in a native perennial, elevating its ability to compete with exotic annuals for water and resources (Zink and Allen 2002). It is possible that carbon addition will behave differently in arid ecosystems due to factors such as a slow decomposition rate. Furthermore, there is potential for these large, physical substances to have other effects, especially on an experiment which is seeded rather than planted. The bark or straw could have compounding effects such as shading the surface, protecting seed, or slowing water evaporation.

Past studies have shown suppression of exotic species by adding around 1150 g C / m² (Reever Morghan and Seastedt 1999; Alpert and Maron 2000; Paschke et al. 2000). Studies show that native plants are facilitated when even higher levels of carbon are added (over 5,000 g C / m²) (Blumenthal et al. 2003; Perry 2001). However, Blumenthal et al. (2003) postulate that the quantity of carbon source necessary to produce these results for less fertile sites, such as those found in deserts, will be much lower.

The two main carbon additions used in the literature are sawdust and sucrose, and both have proven effective. Because sawdust is a waste source, it is more practical and inexpensive than sucrose. In experiments with carbon addition, McLendon and Redente (1992) applied 160 g of sucrose/ m²/ year while Wilson and Gerry (1995) applied 400 g sawdust/ m²/ year, and both experiments saw a reduction in soil nitrogen. Other experiments utilized a combination of sucrose and sawdust. For a Boulder, Colorado, grassland study, Reever Morghan and Seastedt (1999) applied 200 g of sucrose every
month for five months and 325 g of sawdust twice during that time period and saw similar results.

Desert Pavement

Half of all arid land in North America is covered by desert pavement (Evenari 1985), a one or two stone thick mosaic embedded on the surface of a fine grained vesicular layer (Av horizon) of soil (Mabbutt 1965, 1977; Cook and Warren 1973). Desert pavement landscapes are commonly characterized by large swaths of flat pavement areas with little plant life adjoining clusters of shrubs on open ground (Musick 1975). Desert pavement is referred to by a variety of different names depending on its form and where in the world it is located. For example, desert pavement in Australia is called “gibber” (Dixon 2009). In the Saharan Desert, pavement consists mainly of rocky outcrops and is called “hamada” (Mabbutt 1977). In the old world, the word “reg” refers to pavement comprised of small gravel, and reg found within the Sahara Desert is called “serir” (Dan et al. 1982; Amit and Gerson 1986; Mabbutt 1977).

There have been many theories on the formation of pavement, and, until the last couple of decades, it was generally believed that the expansion and contraction of clay particles in the soil caused coarser fragments to be driven slowly to the surface, resulting in large fragments congregating on the soil surface in a smooth mosaic of stone (Quade 2001). It is now widely accepted, however, that pavements are “born at the surface” over millennia by the deposition of aeolian dust that filters under a surface layer of stone, thus lifting it away from the parent material it originally derived from (Wells et al. 1995). The slow formation process of pavement and the Av horizon can take between 4,000 and 10,000 years (Young et al. 2004), and many Mojave Desert pavement surfaces, especially
those at elevations below 400 m, have been dated back to the Pleistocene (Quade 2001). It is thought that the Pleistocene-to-Holocene climate change, a time when dust influx was high due to the desiccation of pluvial lakes, greatly accelerated the formation of Mojave Desert pavements (McFadden et al. 1998).

As pavements age and develop, the hydraulic conductivity of the soil below decreases, resulting in lower water infiltration and increased water runoff (Young et al. 2004). Consequently, less water reaches plant roots, and salts build up in the soil. Shreve (1951) found that, in general, soils below pavement are more saline than bare surrounding soils. Soils under older areas of pavement also have higher clay and silt content which causes them to retain water longer near the soil surface. Young et al. (2004) propose that this might actually reduce drought vulnerability in resident flora by allowing plants longer to transpire water. It is likely, however, that the opposite is true, and the water close to the soil surface has a higher evaporation rate, resulting in lower water-availability for plants (Musick 1975). Shafer et al. (2005) found that, when comparing pavement sites aged from 30 years to 125,000 years old, winter annual plant density was interrelated with pavement age, with higher densities found at the younger sites. Following heavy rainfall, winter annuals are often observed in abundance on pavement surfaces, and wildflowers such as white easterbonnets (Antheropeas lanosum) often cover pavement areas in the spring (unpublished observations). Certain plant species have also been linked to pavement; the few southern Nevada collections of crowned muilla (Muilla coronata) were all taken on either gravelly slopes or pavement (Wesley E. Niles Herbarium 2010).
It is more common, however, to see expanses of desert pavement that are generally devoid of vegetation, possibly due to the inability of seeds to adequately wedge into the surface in order to germinate. High water runoff and low water penetration make the soils under desert pavement a poor germination environment for seeds that do find their way into the cracks of pavement (Shreve 1951). Large expanses of desert pavement exhibiting low plant establishment may play an important role in preventing the spread of invasive species. Protection of these surfaces is inexpensive compared to eradicating established invasive populations. This is important to note because recovery rates for pavement are in the order of centuries. Furthermore, the conditions for formation may no longer be present in the current geologic climate, making recovery of disturbed pavement virtually impossible (Prose and Wilshire 2000).

Biological Soil Crust

Biological soil crusts are complex associations of cyanobacteria, green algae, lichens, and mosses found on the soil surfaces covering interspaces between higher-level plants (Belnap et al. 2001). They occur in all arid and semi-arid regions of the world, ranging from woodland to tundra to desert. The names biological, cryptogamic, cryptobiotic, microbiotic, and microphytic soil crusts are used interchangeably (Belnap et al. 2001).

Literature on biological soil crusts is contradictory as to their supportive or inhibitory effects on higher plants (Serpe et al. 2006; Serpe et al. 2008; Belnap et al. 2001). This is probably due to the heterogeneity, including varied topography and species composition (Belnap et al. 2001), of these living soil surfaces. In a study comparing grass establishment on crusts made up primarily of short moss (Bryum
argenteum) versus crusts of tall moss (Tortula ruralis), Serpe et al. (2006) found that only the short moss-dominated crusts had an inhibitory effect on grass germination. The tall moss-dominated crusts only delayed germination, a factor attributed to higher water content accumulated as seeds slowly fell through the tall moss canopy (Serpe et al. 2006). Serpe et al. (2006) concluded that structural characteristics differing among crusts can have differing effects on seed germination.

The biotic makeup of each particular crust also influences its effect on plant establishment. A study (Serpe et al. 2008) comparing annual grass establishment on a mixed crust composed of both lichens and mosses and on a crustose lichen-dominated crust (Diploschistes muscorum) found that germination was significantly lower on the lichen crust than either the mixed crust or bare soil. The presence of D. muscorum in the lichen-dominated crust suppressed grass establishment by reducing seed germination and root penetration (Serpe et al. 2008). Dominance of different biotic components in the crust has been linked to microhabitat; mosses and liverworts favor more mesic sites, cyanobacteria exists on the most ecologically challenging sites, and lichens favor an intermediate between the two (West 1990).

The positive effects that crusts have on plant establishment are attributed to the many key roles they play in community functions, including soil moisture retention, nitrogen fixation, weed suppression, and protecting the soil from erosion (Eldridge and Greene 1994). Negative effects in the literature are often associated with soil exudates released by crust components (West 1990), the physical barriers crusts form (Romao and Escudero 2005), and crust components competing with seedlings (Belnap et al. 2001). Belnap et al. (2001) found that germination of exotic species was lower on sites with
well-developed biological soil crusts, suggesting that intact crusts may play an important role in preventing invasions. Conversely, exotic plant invasion often results in reduced cover of biological soil crusts (Belnap et al. 2001).

Although biological soil crusts are found only in the top 3 mm of soil, Belnap and Gillette (1998) found that intact crusts were capable of withstanding wind gusts far higher than that ever experienced at their study sites. When the integrity of the crust was compromised by disturbance, the stability thresholds fell below typical wind speeds, leading to further degeneration of the soil surface. When the crust was destroyed, it left the land below completely open to erosion pressures (Belnap and Gillette 1998).

Recovery of biological soil crusts from disturbance takes longer in areas of lower rainfall. For example, on the Colorado Plateau, it may take 250 years for crust to recover while it might take disturbed crusts in the northern Great Basin only 50 years (Belnap and Warren 2002). The Mojave Desert is far more arid than these other regions, and Belnap and Warren (2002) estimate that it could take 2,000 years for disturbed Mojave Desert biological soil crusts to fully recover. Full recovery depends on the recovery of each of its living components. When Belnap and Warren (2002) compared Mojave Desert biological soil crusts that had seen heavy vehicle traffic 50 years prior to adjacent intact crusts, the biomass of cyanobacteria in disturbed crusts had only half recovered. Crust recovery, especially in hot deserts, relies on cyanobacteria colonizing before moss or fungi begin to establish. Belnap and Warren (2002) estimate that full recovery of cyanobacteria at their site would take 85 to 120 years. For lichens inhabiting the fertile islands under plants, they estimated that full recovery would take another 100 years;
lichens in the open spaces between shrubs would take over 1,000 years, as much as two millennia for the more sensitive lichen species (Belnap and Warren 2002).

Literature Cited


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CHAPTER 3

MANUSCRIPT: RELATIONSHIPS OF EXOTIC PLANT INVASIONS WITH BIOLOGICAL SOIL CRUSTS, DESERT PAVEMENT, AND SOIL CARBON IN THE EASTERN MOJAVE DESERT

Abstract

Plant community invasibility is a key topic in the Mojave Desert where exotic species invasions result in new fire regimes and reduced plant diversity. This project consisted of three components: a greenhouse experiment, a field experiment, and a correlational field study. These studies examined how soil surface types (biological soil crust, desert pavement, and open) affect the establishment of three exotic plant species (*Bromus rubens*, *Schismus* spp., and *Brassica tournefortii*) in Lake Mead National Recreation Area in the eastern Mojave Desert. The effects of carbon addition and disturbance on the establishment of these species were also examined. The results of this study showed a correlation between carbon addition and the reduction of density and biomass in all three exotic species studied. Disturbance had no significant effect on establishment, and exotic establishment was generally higher on open surfaces than biological soil crust and higher on biological soil crust than pavement. Species composition showed higher annual plant cover on open sites than biological soil crusts and higher cover on crusts than pavement. Both crusts and open surfaces had higher species diversity than pavement, and annual plant community composition was significantly different on biological soil crust and pavement. Protection of biological soil crust and desert pavement in conjunction with carbon addition could serve as useful tools for reducing the spread of invasive species in the Mojave Desert. These findings are
expected to contribute novel information to the broader understanding of these factors in arid lands as well as provide information applicable for local land managers that are tasked with protecting desert soil surfaces and minimizing the impacts of exotic species.

Introduction

Exotic species invasions are a global issue, affecting native biodiversity and resources. Consequently, community invasibility has become a major focus in ecology. In the deserts of southwestern North America, exotic annual grasses are creating brand new fire regimes which then level established native plant communities (D’Antonio and Vitousek 1992). These exotics also displace native species and change soil properties (Belnap and Philips 2001). Our understanding of exotic plant invasions in deserts is still limited. Even if large sums of money became available to land managers, they would not know which techniques were the most effective in reducing community invasibility.

Two factors that affect community invasibility are soil surface characteristics and nutrient availability. Biological soil crusts and desert pavement can both be loosely defined as soil surfaces. In deserts, biological soil crusts are formed by a mutual association of lichen, moss, and cyanobacteria (Belnap 2003). Desert pavements are primarily found in hot deserts, and they are essentially mosaics of stone over relatively stone-free soil (Cooke 1970). Carbon has been added as an antifertilizer in past experiments in order to manipulate nutrient availability (Blumenthal et al. 2003). These three factors will be discussed in the following paragraphs.

The small amount of available research on plant establishment on biological soil crusts is contradictory (Belnap et al. 2001). Crusts can increase the water-holding capacity of soils and provide microsites for germination. On the other hand, many
species, including annuals, have difficulty germinating in areas with low soil disturbance, stabilized soils, and low litter, and these are often characteristic of sites covered by biological soil crusts (Belnap et al. 2001). Germination on crusts can be reduced particularly for species that lack seed burial mechanisms (i.e. rodent caching); this includes some exotic annual grasses which may have evolved in livestock-disturbed areas (Belnap et al. 2001). Some hot desert studies have reported that crust inhibits plant establishment (Serpe et al. 2008; Serpe et al. 2006) while others have reported just the opposite (Belnap et al. 2001). If crusts are found to limit exotic plant establishment, research that contributes to our understanding of effects that crust has on plant establishment could play a key role in managing community invasibility. According to Bowker (2007), soil crusts have the potential for rehabilitation. A strategy for limiting exotics involves strengthening existing native soil surfaces and plant communities to make them less susceptible to invasion.

The literature is more straightforward about the relationship between desert pavement and plant establishment. Large areas of pavement are visibly devoid of plant life. This may arise from lowered water infiltration capability or from the prevention of contact between the seed and soil (Wood et al. 2005). When pavement is disturbed by either anthropogenic or natural processes, these areas are more able to support plants, including exotics (Haff 2001). It follows that maintaining intact pavement is an important method for limiting exotic establishment. There is little research into the feasibility of recreating or accelerating the formation of pavement (Abella et al. 2007), but restoring and maintaining intact pavement could be a future management goal.
In restoration, carbon is sometimes added to soils in the form of straw, wood chips, sawdust, or sugar. It acts as an antifertilizer and decreases the availability of nutrients in soil. Soil microbes consume the carbon added, and, in turn, also consume nitrogen and other nutrients, resulting in a lowered availability of these resources to plants. Exotic plants, such as those studied here, are often limited by resources, and lowering soil fertility through carbon addition has been successful at reducing exotic establishment in more mesic environments (Zink and Allen 1998; Morgan 1994; Reever Morghan and Seastedt 1999; Alpert and Maron 2000; Paschke et al. 2000). It is important to be aware that carbon addition could also affect other nutrients, soil pH, waterholding capacity, and soil surface microsites. It is only an option if the overall effect of carbon addition is positive and side effects are acceptable. Literature on the effects of carbon addition is still rather contradictory, much like that for biological soil crusts (Alpert and Maron 2000). One explanation is that previous studies may not have added enough carbon to produce a response (Blumenthal et al. 2003). Carbon addition has also been insufficiently documented in deserts (Brooks 2003).

The three factors of biological soil crust, desert pavement, and carbon addition could each affect the establishment of exotic plants, potentially with a species-specific outcome. An integrated approach is proposed with both field and greenhouse experiments to help strengthen the results. The three exotic annual species (*Bromus rubens*, *Schismus* spp., and *Brassica tourneforttii*) used are priority species of concern in the Mojave Desert. It is hypothesized that (1) biological soil crusts will have a species-specific effect on exotic plant establishment, and that they will overall decrease exotic plants; (2) exotic plant establishment will be decreased by desert pavement; and (3)
carbon addition will hinder exotic species establishment on open soil but will have less of an effect on crust and pavement.

All three invasive species used in this study are winter annuals of Mediterranean origin. The biological soil crusts used in both the field and greenhouse experiments are lichen-dominated, lacking well-developed moss or cyanobacteria components. Lichen genera present are *Collema*, *Placidium*, and *Peltula*, all common in low-elevation Mojave Desert habitats.

Methods

Field Experiment

This experiment looks at real-world conditions and serves as an appraisal of how the greenhouse experiment represents field conditions. It is also an assessment of the affect that disturbing the surface treatment has on invasibility, a component that could not be included in the greenhouse experiment.

This three-factor, factorial design consists of two levels each of biological soil crust (disturbed or intact), desert pavement (disturbed or intact), and carbon addition (added or not). This makes a total of eight treatment combinations with four replications each to make 32 experimental units. There were also four replications each for pavement and crust of unseeded control plots.

Study Area

Studies were located within Lake Mead National Recreation Area (LMNRA) within the eastern Mojave Desert (Table 1; Figs. 1-2). The Mojave Desert is the driest desert in the southwestern United States; LMNRA receives an average of 14 cm of rain annually (Western Regional Climate Center (WRCC), Reno, NV). The eastern Mojave
Desert relies mostly on winter precipitation between the months of October and April with light monsoon-season precipitation from July to September (WRCC). Las Vegas area temperatures range from a low of -7°C in December to a high of 45°C in July (WRCC). LMNRA is dominated by the creosote-scrub plant community, typical of elevations below 1200 m within the Mojave Desert (Craig et al. 2010). In the Mojave Desert, exotic annual plant species comprise a greatly disproportionate percentage of total annual plant biomass compared to the small proportion of annual plant species that they represent (Craig et al. 2010).

The field portion of the study occurred at an elevation of 633 m off of Bittersprings Road (AR 101) within the LMNRA (Table 1; Figs. 2-3). This 0.4-ha site is within a creosote-scrub community. Although gypsum outcrops are present at the site, the experimental plots were set up on soil more alluvial in nature. The crust at this site is sprinkled with rocks ranging in size from 1 to 5 cm, and the crust is not always evenly spread across units, leaving some bare areas. The site was relatively flat with minor slopes across units. All three of the target invasives (Bromus rubens, Schismus spp., and Brassica tournefortii) were already present in abundance on the site prior to this study.

Unit Setup

The study area consisted of 32 individual field plots, each 1 m² with at least 1 m buffers. In addition, there were eight control plots (receiving no treatment or seed) which served as a base point from which to determine the typical biomass and plant diversity for both pavement and crust at the site. This is especially relevant for determining to what extent seed of the three target invasives was already in the seedbank and was not a result of experimental seeding. Sites were chosen on level ground and were not in washes or on
gypsum outcrops. Due to the patchy nature of study material, the units were placed depending on the availability of surface types. An effort was made to intersperse pavement (Fig. 4) and crust (Figs. 5-6) plots throughout the field site. Additionally, the dimension of crust units varies depending on available surfaces. The majority of units were 1 m × 1 m in shape but necessity dictated that some of the crust units be 1.5 m × 0.67 m or 1.25 × 0.80 m (Figs. 5-6). However, the area of every unit is 1 m². The treatments were randomized.

First and Second Rounds of Seeding

Due to low emergence during the first round of seeding (Figs. 7-8), a second round of seeding was done the following year. When tested, *Brassica* and *Bromus* had about 60% seed viability, so it is likely that it is, instead, environmental factors that are the cause of the low establishment recorded during the first round. The viability of this seed was tested by wrapping 50 seeds per species in moist paper towels and placing these inside a plastic bag in a warm, humid greenhouse environment. Seed was monitored for germination every few days, and paper towels were moistened periodically. *Bromus* seed was tested both with this paper towel blotter method and by seeding soil-filled pots. *Schismus* seed had a lower viability than that of the other two species, with 16% germination averaged from both the paper towel and soil planting methods. The second round of seeding utilized the same *Brassica* seed, and it is logical that viability levels remained similar six months after initial viability tests were done. *Bromus* and *Schismus* seed used in the second round were collected in June of 2009 from seed at the field site. This may have resulted in a higher viability; for example, studies of *Bromus* seed have
shown 100% seed viability at maturity (Wu and Jain 1979), followed by a substantial drop in viability during subsequent years of storage (Jain 1982).

The first round of seeding took place on February 14, 2009, and the second round of seeding took place November 10, 2009. There were two main differences between the two rounds of seeding that most likely accounted for the difference in emergence levels between the two years: the month the seeding took place and low winter precipitation levels. The first round of seeding took place too late in the season, hence it did not benefit from germination cues and early winter rain. This was corrected for in the second round, as seed was laid down in the fall. All three winter annuals studied typically senesce by May. The second round of seeding was also during a wetter year; according to nearby Valley of Fire State Park climate center (WRCC), rainfall at the site was between July 2008 and June 2009 was 13.8 cm while rainfall from July 2009 to June 2010 was 15.4 cm. Both years, precipitation occurred mostly from December to March. For the first round of seeding, the amount of rain that fell between seeding and surveying was only 4.1 cm while second round received 14.3 cm between seeding and data collection. Due to minimal first round data (Figs. 7-8), all the data used for this study are second round data. Seed from the previous round would, theoretically, still be present in the seedbank of each plot, doubling potential densities.

It is possible that some seed from round one germinated during the first year but did not emerge, making the available seed count per plot during the second round uneven. This would follow similar trends to those probably also happening in the soil seedbank. According to the results of percent cover data collected after the first year, very little seed emerged from round 1. Germination of seed during the first round can be grouped
together with other factors such as granivory from ant activity and wind blowing seed off the experimental plots.

Treatments

**Disturbance**

For the disturbed treatment, disturbance was simulated by hand raking to a depth of 2 cm. This was achieved by moving a hard, metal rake across the surface in rows, tearing the crust or pavement so that the entire unit surface was consistently disturbed. For treatments that got both carbon addition and disturbance, the disturbance was simulated before the carbon was applied. Both treatments of disturbance and carbon addition were done on February 13th one day before the first round of seeding and nine months before the second round of seeding.

**Carbon Addition**

Carbon sources are untested in arid environments and there was uncertainty as to whether sawdust or wood chips would break down into the soil during the necessary time frame. Sawdust is a more practical carbon source than sucrose for the use of land managers, but past studies required tilling it into the soil (Blumenthal et al. 2003; Alpert and Maron 2000; Corbin and D’Antonio 2004). Because intact soil surfaces and their effects on invasibility were being studied, this disturbance of the soil surface would have compromised the experiment. In order to minimize these confounding factors, the decision was made to use sucrose because it would break down faster, becoming immediately available to soil microbes and tying up nitrogen quickly.

The carbon source was a sucrose-water solution made from table sugar. To each appropriate experimental treatment plot, 3 L sucrose was mixed with an equal amount of
water in a hand sprayer and then applied to plots in a steady spray that was not hard enough to disturb crust surfaces. At the time, winds were minimal and the spray was applied close to the soil surface. The amount of carbon applied, an equivalent to 1263 g carbon / m\(^2\), was slightly higher than the average amount past studies found reduced exotic establishment for more fertile ecosystems (Reever Morghan and Seastedt 1999; Alpert and Maron 2000; Paschke et al. 2000). Due to lower existing fertility levels, it is likely that less carbon is necessary to see similar results in the Mojave Desert.

Following is a description of how the amount of carbon was determined. Assuming about 2% of Mojave desert soil is organic matter and roughly half of that is carbon, an application of 10 times the amount of carbon already present in soil would be enough to yield significant results. Assuming carbon is needed to reach 2 cm depth in the soil, over 1 m\(^2\), the amount of carbon (1%) would be 200 cm\(^2\). Because the density of sugar is 1.5 g / cm\(^2\), 300 g sugar would be equal to 1% of soil carbon. Ten times that would be 3000 g of sugar per unit. This is roughly equal to 3 L. To offset this application, 3 L of water was also applied to each of the units that did not receive the carbon addition and also to the 8 control units. This sucrose-water solution application was applied during a cloudy day while temperatures were at around 10\(^\circ\)C.

**Seeding**

Following treatment applications, seed for all three invasive species were sown together on the soil surface of all plots (control plots remained unseeded). A seed density of 99 seeds / m\(^2\) was applied during the first round then a second time 9 months later for the second round, with a total possible added seedbank of 198 seeds / m\(^2\). The seeds used were collected within L MNRA. To simulate natural conditions, seeds were not watered
in. All three seed species were cleaned prior to sowing so that an exact amount of 33 seeds per species could be accurately applied to each unit during each round.

There are morphological differences between the seed of each species that could affect the experimental results. This study compares the establishment of two monocot grasses (*Bromus* and *Schismus*) with a dicot (*Brassica*), and only the *Brassica* “seed” was the actual seed. For the two grasses, the entire fruit (hereafter referred to as seed) was applied, and this could modify germination, growth rate, or penetration. *Bromus* seeds are about 11 mm long and consist of a caryopsis attached to a long awn, presumably to allow it to catch the wind more easily. When placed on a pavement unit, the *Bromus* seeds lay on the surface and gave the impression of being easily blown away by wind. It also seemed that, when placed on disturbed soil, the seed gained more connection to the soil (especially moist soil), making it easier to get a foothold. *Schismus* seeds are fine, dust-like particles. When seeding plots, this seed was hard to control. Although an effort was made to evenly distribute seed, these may have fallen anywhere within the plot, potentially even in one cluster. *Brassica* seeds are spherical and about 1 mm in diameter. When seeding plots, *Brassica* seed hit the surface of the crust or pavement then rolled into any crevice, lodging itself. It is possible that the physical properties of the seed will affect the experimental results because the species whose seed stays in the plots will have a greater potential for germination than the species whose seed blows away with the first winds. Ants were also observed at the site, and there is the possibility of granivory.

Data Collection

Density and biomass of the three exotic species were collected for all the plots, including unseeded controls. Although *Brassica* was seeded at the site, establishment
was so low (3 plants for the entire field site) that it was not included in the field study results. Plant biomass samples were collected dry and then dried in an oven for 24 hours at 60°C. Second round data were collected on May 10, 2010. In addition, cover class data was collected for all annual species (native and exotic) found on the treatment plots in May 2009. Further details on the cover class data collection can be found under “Correlational Field Study – Community Study”.

Greenhouse Experiment

The goal is to examine how biological soil crusts, desert pavement, and carbon addition affect the establishment of three exotic species. The experimental layout is a factorial experiment including three levels of soil surface (biological soil crust, pavement, and open), two levels of carbon addition (added or not), and three levels of exotic species (Bromus rubens, Schismus spp. and Brassica tournefortii). There were 18 treatment combinations with four replications for a total of 72 experimental units.

Surface Soil Salvages

In order to perform the greenhouse experiment, material had to be collected from the field. Desert pavement, biological soil crust, and soil surfaces that were neither pavement nor crust (designated open) were collected from areas near Northshore Drive in LMNRA that were slated for realignment construction (Table 1; Figs. 9-11). Salvages took place between the months of September and November, 2008.

Desert pavement material was collected from a site within the Valley of Fire Bridge road realignment zone at an elevation of 424 m. The crust material and open material were both collected near the Overton Beach turnoff at 427 m elevation. The crust was salvaged from gypsum soils while the open material was salvaged from a
nearby non-gypsum area. Due to the nature of the available material within the road realignment zones, crusts were on gypsum soils while pavement was on non-gypsum, more alluvial soils. The open site had a thin layer of undeveloped crust on top.

Salvaged soil surfaces included the upper 10-15 cm of soil, intact. Salvages were collected with a flat shovel, and put into individual plastic flats (Fig. 12). Every effort was made to keep the soil surface intact though practicality suggested that some breakage would occur. For the desert pavement salvage, surface stones from pavement within a meter of the salvage area were collected to fill in the gaps. The best efforts were made to return the pavement back to its previous intact state; however, it was not possible to recreate its previous, unbroken surface. For the crust salvage, an effort was made to place pieces of crust onto all exposed surfaces, but small gaps remained between pieces. Once salvaged, the flats, carried on 0.3 × 0.6 m pieces of plywood, were loaded onto a truck. Packing blankets were placed underneath, above, and layered between board-flat combinations. The salvage (Figs. 13-15) were kept dry until the experiment commenced.

Greenhouse Setup

Experimental units were housed in individual black plastic 0.25 × 0.51 × 0.05 m flats. They were arranged randomly on greenhouse benches and treatments were also assigned randomly. Carbon and/or seed were added/sown in the appropriate flats.

The carbon source of table sugar was layered over applicable units and then watered in (flats that did not receive this treatment received an equal amount of water). This solid carbon application, in contrast to the dissolved solution applied at the field site, was necessary because water running out the bottom of the flat would carry the sucrose
with it if a dissolved solution was applied. In order to determine whether the sucrose was immediately leached through, buckets were placed underneath the flats during the initial watering in of the carbon addition. The collected water – by visual observation, touch, and taste – did not have sucrose in it. At the field site, applying sucrose in a dissolved solution was necessary because then it would be immediately absorbed into the soil and begin to be broken down by soil microbes. The amount of carbon to be applied to each greenhouse unit was slightly higher than in the field experiment given that some leaching from higher watering levels would occur. Sucrose in the amount of 0.5 L per flat was applied followed by 0.5 L water. This is an equivalent of 210 g of carbon / flat or 1615 g of carbon / m².

Seed was sown at a density of 25 seeds per experimental unit or 192 seeds / m². Seed per species for each plot/flat were approximately the same for both the field and greenhouse experiments (33 versus 25). Data collection included the density of each species in each flat. For example, for flats that were seeded with *Bromus*, the densities of *Schismus* and *Brassica* were collected in addition to *Bromus* density. This was done because *Bromus* and *Schismus* were observed together on many flats, potentially a result of an existing seedbank in the soil. Flowers were clipped before going to seed in order to avoid contaminating the greenhouse environment, precluding a biomass collection.

First and Second Round Data

Like the field experiment, the greenhouse experiment was repeated twice. The carbon treatment was added to the flats on March 2, 2009, and following that, flats were seeded and the first round began. Seed was used from the same batches as for the field experiment. The greenhouse temperature remained around 30°C for the duration of both
experimental rounds, sometimes reaching as high as 35°C. Minimal emergence occurred during the first round of seeding, probably due to insufficient water received. During the first round, flats were watered every other day, skipping weekends. Data were collected on July 22, 2009, after about 4 months, and due to low densities averaging 1.5 plants/flat for *Bromus*, 0.4 plants/flat for *Schismus*, and 0 total plants for *Brassica*, the data were rejected.

The second round of seeding took place on November 4, 2009 and final data were collected on February 26, 2010, a time period of about 4 months. For the second round, an overhead irrigation system with spray-type watering was installed (Fig. 16). It went off for 2 minutes every 8 hours. The second round produced substantial data. Because there were two rounds, there were two sets of seed in the soil of each flat for a total of 50 seeds per flat. The minimal data from round 1 were discarded, and only round 2 data were analyzed.

**Correlational Field Study – Community Study**

The goal of the correlational field study was to compare annual plant community composition by soil surface (crust, pavement, and open) in non-manipulated systems. Study Sites

This study consisted of four sites (Table 1; Fig. 17). The first was at the Bittersprings Road site previously used for the field experiment, and annual plant species composition data were collected both from control plots and from the experimental plots previously used. The three other sites were separated physically by at least 1.5 km or by significant soil type differences. Sites 2 and 3 were geographically close, but Site 2 was located on gypsum in order to include data comparing gypsum annual plant communities
on crust, pavement, and open surface areas. Each site consisted of three 1 m² plots of each of pavement, crust, and open surface areas. An effort was made to intersperse plots of these three surface types at each site.

Data Collection

The community surveys took place in May 2009, and all sites were sampled on the same day. The plots were marked (rebar hammered down) to facilitate visitation in the future. Cover classes were documented for all annuals species found within each plot. The result was two sets of data – one for the field experiment plots and the other set of unseeded control plots at four different survey sites. Cover classes were: 0-1%, 1-2%, 2-5%, 5-25%, and >25%. The results for the experimental plots are included under the field experiment results.

Species encountered in the community survey (Table 14) were submitted to Dr. Wesley Niles, an expert in eastern Mojave Desert flora, for identification. Nomenclature follows the United States Department of Agriculture’s Natural Resources Conservation Service Plants Database. Voucher specimens are housed in the Wesley E. Niles Herbarium at UNLV.

Data Analysis

For the field experiment, *Bromus* and *Schismus* were analyzed separately. The log₁₀ +1 transformed density and total biomass values were analyzed in an analysis of variance (ANOVA) with surface type, disturbance, carbon addition, and all possible interactions among them modeled as fixed effects in SAS v9.1 (PROC MIXED; SAS Institute 2002-2004). Some treatments resulted in no emergence of plants, making the data heteroscedastic. However, p-values obtained from permutations agreed with p-
values derived with ANOVA assumptions in every case (data not shown), so the latter are reported for simplicity. The average biomass of individuals of each species was also compared. Because many treatment combinations in the field experiment did not produce plants, the number of terms in the models was reduced (see results). The *Schismus* model contained only surface type, disturbance, and their interaction. The *Bromus* model was used to test the effect of surface type, disturbance, and surface type by disturbance when no carbon was added. The *Bromus* model also contained the effect of disturbance with carbon addition when biological soil crust was present. Post-hoc comparisons were adjusted using the Bonferroni method, and least-squares means and standard errors (derived from the minimum adequate model when available) were back-transformed when appropriate.

To explore the species composition differences among surface types and treatments at the field experiment site, non-metric multidimensional scaling (NMS) ordination was used, on auto-pilot thorough mode, in the software PC-ORD (McCune and Mefford 1999). Percent cover was calculated by taking the midpoint of the cover class category, and then the percent cover was relativized in order to compare across plots. Species composition was ordinated with surface type and treatment variables input as a second matrix for creating vectors that showed strong correlations.

In order to test the null hypothesis of no difference in species composition among surface types and treatments, separate multi-response permutation procedure (MRPP) analyses were run using different plot by species data matrices (e.g. crust/pavement/open and relative percent cover) (McCune and Mefford 1999). The purpose in these analyses was to compare species composition among surface types and treatment combinations.
Relative percent cover was used to assess differences in community composition among surface types and treatment types. If an overall MRPP test among treatments was significant, pairwise tests were used for multiple comparisons (McCune and Mefford 1999).

Sørensen distances and PC-ORD default group weightings were used for all MRPP analyses (McCune and Mefford 1999). Multi-response permutation procedures also provide an A-statistic, the chance-corrected within-group agreement, which provides an estimate of the effect size that is independent of the sample size. A is maximized at 1 when all plots within groups are identical, but in community ecology, A is commonly below 0.1 (McCune and Mefford 1999).

For the greenhouse experiment, seedling emergence was analyzed separately for each species in ANOVA models with surface type, carbon addition, species that was seeded, and their two- and three-way interactions, as fixed effects. Significance was derived from 10000 permutations. Pairwise comparisons were computed for significant effects ($\alpha = 0.05$) and tested by permutation. Means were computed for each group, and error (95% confidence interval by quantile) was estimated using 1000 bootstrapped samples.

For the community survey study, total cover ($\log_{10} +1$ transformed) was analyzed in a mixed model ANOVA with surface type as the lone fixed effect and site, plot within site, and plot within site by surface type (the denominator for the surface type effect) as random effects. For the community survey study of the field experiment plots, exotic species, native species, and total cover were analyzed for differences by carbon addition and disturbance in a mixed model ANOVA. Species richness (number of species / 1 m$^2$)
plot) was analyzed in a generalized linear model (GLM) with poisson errors with terms defined as for the total cover model. Exotic cover and the percent of forb cover relative to total cover were analyzed after arcsin-square-root transformation in a mode identical to the one for total cover. Analyses were conducted in SAS v9.1 (SAS Institute 2002-2004). Significant effects were tested using a Tukey post-hoc analysis ($\alpha = 0.05$).

To explore the species composition differences among the four sites sampled during the community survey study and between surface types, non-metric multidimensional scaling (NMS) ordination was used in auto-pilot thorough mode, in the software PC-ORD (McCune and Mefford 1999). Percent cover was calculated by taking the midpoint of the cover class category, and then the percent cover was relativized in order to compare across plots. Species composition was ordinated with site and surface type variables input as a second matrix for creating vectors that showed strong correlations.

In order to test the null hypothesis of no difference in species composition among sites and surface types, I ran separate MRPP analyses using different plot by species data matrices (e.g. crust/pavement/open and relative percent cover) (McCune and Mefford 1999). My purpose in these analyses was to compare species composition among surface types. I used relative percent cover to assess differences in community composition among surface types. If an overall MRPP test among treatments was significant, pairwise tests were used for multiple comparisons (McCune and Mefford 1999). I used Sørensen distances and PC-ORD default group weightings for all MRPP analyses (McCune and Mefford 1999).
Results and Discussion

Field Experiment

*Bromus*

Disturbance, alone or in combination with surface type or carbon addition, had no impact on the density or total biomass of *Bromus* individuals which germinated and established (Tables 2, 3). Significantly more *Bromus* individuals were observed on biological soil crusts (6.42 (1.15, 1.37) individuals; mean (lower SE, upper SE)) than on desert pavement (0.60 (0.25, 0.29) individuals) (Table 2; Fig. 19). There were more individuals on surfaces that were not treated with carbon (4.78 (0.90, 1.06) individuals) than on surfaces with carbon addition (1.05 (0.32, 0.38) individuals) (Table 2; Fig. 19). The main effects observed were surface type and carbon addition for both the number of individuals and total biomass (Tables 2-3). There was also a significant interaction between surface type and carbon addition for total biomass, with biomass far greater on crust with no carbon addition than for any other treatment (Table 3; Fig. 18).

*Schismus*

*Schismus* density and overall biomass were impacted solely by carbon addition (p = 0.0000) (Tables 4-5; Fig. 20). There were no observed impacts of surface type or disturbance, alone or in combination with any other effect. There were significantly fewer individuals in areas treated with carbon (6.30 (1.73, 2.27) individuals) compared to those that were not (0.04 (0.25, 0.32) individuals), and biomass followed the same trend (no carbon added: 0.18 (0.05, 0.05) g; carbon added: 0.00 (0.04, 0.04) g). Because the carbon addition virtually eliminated successful establishment of *Schismus*, average size
was compared for surface types and disturbance regimes when carbon had not been added. Neither surface type nor disturbance affected the average size of Schismus (Table 6).

**Brassica**

Because there was negligible Brassica germination (3 plants for the entire site), it was not included in the field experiment analysis.

**Community Composition**

There was no difference in annual total plant cover on field experiment plots between either levels of carbon addition or disturbance treatments (Table 12). In analyzing the results of the annual plant survey, there were interactions between disturbance and surface type ($A = 0.063; p = 0.0048$) (Fig. 28). Differences in community composition were found when comparing both intact and disturbed crust communities to both intact and disturbed pavement communities ($p$ values between 0.0015 and 0.042). Likewise, in the interactions between carbon addition and surface type ($A = 0.103; p = 0.0032$), differences were found between plant communities on crust (both with carbon added and without carbon) and communities on pavement (both with carbon added and without carbon) ($p$ values between 0.00073 and 0.042) (Fig. 29). There was no difference in community composition between plots disturbed and undisturbed and between those with carbon added and without carbon.

**Greenhouse Experiment**

Species varied in their response to the treatments, but in every case seeding resulted in more of the seeded species emerging (Table 7; Figs. 21-23).
**Bromus**

Although Bromus emergence was high, it did not exhibit any significant differences between treatments (Table 7; Fig. 24).

**Schismus**

Of the three species studied, *Schismus* was the most sensitive to surface type, with significantly more plants on crust and open surfaces relative to pavement (Table 7; Fig. 25). For *Schismus*, carbon addition reduced the appearance of plants in seeded and unseeded conditions on open surfaces and for seeded conditions on crust (Fig. 25).

**Brassica**

When seeded, there were slightly more *Brassica* plants on open surfaces compared to crusts and pavements. When carbon was added to plots seeded with *Brassica*, establishment of *Brassica* plants was virtually eliminated (Table 7; Fig. 26), and no seedling death was observed before final data were collected.

**Community Composition**

Open surfaces had significantly more annual total plant cover than crust surfaces, which had significantly more total cover than pavement surfaces (Table 8). Species richness was statistically the same between open and crust surfaces and both had more species on average than pavement surfaces (Table 9). There were no significant differences among surface types in their proportion of native forbs or in their proportion of exotic grasses (Tables 10-11).

There were over 17 annual species counted during the community study (Table 13), consisting of two exotic grasses (*Bromus* and *Schismus*) and 15 natives, including the native grass *Vulpia octoflora* var. *octoflora*. There were interactions in plant
community composition based on surface type by site \((A = 0.337; p < 0.0001)\) (Fig. 27). There were significant differences \((p < 0.03)\) in community composition on crusts at different sites. Plant community composition on pavement was similar among sites and surfaces, with the exception being a difference between crust and pavement communities at site 4 \((p = 0.027)\) and a difference between pavement communities at sites 3 and 4 \((p = 0.032)\). Plant community composition on crust was significantly different from composition on open surfaces for three out of the four sites (sites 1, 2, and 4). The only other difference in composition that open surfaces showed was a difference between open surfaces at sites 3 and 2 and sites 3 and 1.

**Discussion**

Examining the role of disturbance in invasibility

Contrary to past studies which have concluded that there is a positive relationship between disturbance and exotic species establishment (Grime 1979), the results of this study showed was no significant difference between establishment on disturbed versus intact plots. It could be that there is no correlation between disturbance and invasion. It is, however, unlikely that this is the case because past literature has shown that disturbance facilitates all three of the invasive exotics studied here (Suazo et al. 2009; Brooks 1998, 1999). Insignificant results could also be attributed to the method of disturbance – hand raking. Many past studies on disturbance have focused on compressional and shear forces such as those from vehicles or past military activity (Prose et al. 1987; Belnap 1996; Belnap and Warren 2002). Experimental studies of disturbance, however, have used the hand-raking method, often in combination with a compression force (Leys and Eldridge 1998; Hawkes 2004). It is more plausible that this
study was too short term to pick up disturbance effects. The desert changes slowly, and possible secondary succession would be on the order of decades or centuries rather than years (Iverson et al. 1981; Webb et al. 1986, 1988; Prose and Wilshire 2000). Data were collected only a year after the disturbance simulation, and it is more probable that disturbances in the desert initially lower plant health. Data collection in future years would likely find that disturbance facilitates these exotics.

During the first round of data collection, there was lower (though not statistically significant) average total coverage of annuals (6.8% versus 9.7%) on disturbed versus intact plots. Because disturbance was done in February, only three months prior to first round data collection, I attribute these results to the damage of seedlings that had already germinated. Data collected the following year, however, still showed little correlation between disturbance and establishment. It is likely that data collected from subsequent years would begin to show a different picture of the relationship between disturbance and exotic establishment.

It is highly likely that succession as it is known in more mesic environments does not exist in the Mojave Desert (Muller 1940; Brooks 1998) or that it happens over centuries (Webb et al. 1987). Consequently, it is reasonable to assume that, at the very least, secondary succession after disturbance is slow and results in low initial species establishment with higher germination rates from colonizers occurring years later. There have not been, however, any studies for arid environments involving establishment data collected yearly following disturbance. It would be interesting to document early secondary succession in deserts. Perhaps if the study were continued, a few years out would result in greater emergence on disturbed than intact surfaces.
Examining the roles of surface types in suppressing exotics

Overall, the study showed significantly less exotic establishment on crust and pavement than on open surfaces. While it is clear that the type of soil surface plays a role in inhibiting establishment of the exotic species studied, the results were somewhat varied. There was some difference between the results of the field and greenhouse experiments for *Schismus*. In the field, *Schismus* establishment exhibited no correlation to surface type, but, in the greenhouse study, there was significantly higher density on open surfaces than on crust and pavement. This could be explained by two different factors. First, it is likely that if open surfaces had been included in the field experiment, *Schismus* would have had lower establishment on crust and pavement compared to open surfaces. Second, this difference is possibly an indicator of water limitation. The greenhouse received regular irrigation, and, consequently, the greenhouse experiment simulated the potential level of *Schismus* establishment in years of high rainfall. However, the field experiment only compared establishment on crust and pavement. If open areas had been studied, it is possible that *Schismus* would have demonstrated a reduced establishment on crust and pavement in relation to open. If *Schismus* is, in fact, limited by water in its response to surface type, this may make surfaces of crust and pavement especially important to protect in order to limit *Schismus* establishment in years of high rainfall.

As can be expected, pavement surfaces greatly reduced the establishment of all three exotic species, in some cases eliminating the exotics entirely. Crust was more effective than open surfaces for reducing exotic establishment. Serpe et al. (2008) found that lichen-dominated crust suppressed exotic establishment more so than a mixed crust
composed of various lichens and mosses. Because biological soil crusts are so heterogeneous, it could be that suppression of invasives in this study can be specifically attributed to the lichen-dominated crust. This indicates an important role played by these two surface types in suppressing exotics, and, therefore, the protection of these surfaces could be an important management tool. Future studies of exotic establishment on crust and pavement in the field should add open surfaces.

An interesting note in the field experiment results was higher *Bromus* and *Schismus* biomasses (as well as *Schismus* density) for the unseeded control plots (both on crust and pavement) than for the experimental plots, regardless of the treatment combinations. Because all the treatment plots received some type of treatment – whether it be actual disturbance, carbon addition, or just seeding - they can be loosely classified as being disturbed to some extent. Consequently, the year following this “disturbance” resulted in an initial lowered establishment on the treatment plots. It is likely that after a few years, growth will reverse and there will be higher exotic biomass and density on these experimental treatment plots than the controls.

The higher exotic establishment on field control plots could also be attributed to targeted granivory on the treatment plots where seed was applied. The control plots would have seed from many previous years buried in the seed bank at different levels and different ages, protecting it from predation. The experimental seed was all spread on the surface of the soil at the same time, and several active ant mounds were observed at the site during seeding. In addition, the ants were seen moving seed. This granivory, possibly in combination with the previously-mentioned disturbance effect, could have resulted in lowered establishment during this initial data collection.
Examining the role of carbon addition in suppressing exotics

Carbon addition also played a strong role in reducing establishment, and, like with surface types, results differed between the field and greenhouse experiments. *Bromus* and *Schismus* establishment were significantly reduced in the presence of carbon in the field experiment, but the greenhouse experiment showed a weaker correlation between carbon addition and the suppression of establishment for *Schismus* and no significant correlation for *Bromus*. This is the probable result of quicker breakdown of carbon in the greenhouse setting than the field. Most likely, the warm, moist environment of the greenhouse promoted increased microbial activity, breaking down carbon faster, and, over time, frequent irrigation leached the carbon from the flats. Between the application of the carbon source and the collection of the second round data, the flats in the greenhouse received several months of regular watering.

Even with the lowered carbon amount, carbon added flats in the greenhouse experiment still saw *Schismus* reduced on open and crust, albeit a lowered percentage than in the field. Furthermore, the addition of carbon virtually eliminated *Brassica* establishment, possibly indicating that the suppression of *Brassica* requires lower levels of carbon source than the exotic grasses do. This is particularly significant in light of the lack of effective control methods for this species.

The differences seen in the greenhouse experiment versus in the field can also be attributed to the nature of the surface material. The surface soils salvaged and used in the greenhouse experiment were not entirely intact nor were they experimentally disturbed. Therefore, greenhouse results should be interpreted as describing the establishment of these species on surfaces which are at a low level of disturbance. At the same time, the
results of the field experiment showed no significance in the differences in establishment after disturbance or in an interaction between disturbance and carbon addition. A difference in biomass on carbon-added greenhouse flats was also observed. Unfortunately, due to the greenhouse nature of the study, plants had to be deadheaded to prevent weed seed contamination, so biomass sampling was not possible, and, therefore there are no data to support this observation.

Because the field experiment responded positively to sucrose that was added to soil surfaces 14 months before data were collected, it follows that sucrose as a carbon addition is successful for at least one year of average Mojave Desert rainfall. Subsequent data collection from the site during following years would show the rate at which the effectiveness of sucrose decreases with time.

The assumption has been made throughout the literature and in this study that effects seen on treatment plots/flats that received a carbon addition are due to lowered soil fertility. There are other possible explanations for results based on the nature of the carbon addition used. Alternate hypotheses relate to physical, chemical, ecological characteristics of sucrose that might affect plant establishment. When wet and spread across a plot, the sucrose forms a sticky coating. This physical layer might help seed stick to the soil surface, but it might also form a barrier to germination. It is also possible that the high sucrose content could dry out the seed by reducing water availability through osmosis, resulting in lowered germination. A further study comparing seedling emergence in sterile soil when sugar-water or regular water is applied would help to determine whether sucrose suppresses seeds through a physical barrier effect or reduced water availability. It is also possible that the presence of sugar could attract insects and
rodents to the plots where carbon was added, leading to targeted granivory at those plots. This is unlikely, but a future study could tally ant visitations at each plot to determine whether some were visited more than others.

Differences in plant community composition by surface type.

In a survey of annual plant community composition, pavement surfaces showed lower plant cover and species diversity than crust or open surfaces, and crust surfaces showed lower plant cover than open surfaces. These findings for pavement are consistent with past literature. It is generally accepted that areas of pavement support sparse plant life. There is less established knowledge about plant cover on crusts, and these results do need feed into any commonly held theories. While crust plots had similar species diversity to open plots, annual plant cover was actually lower on crusts than open. This suggests that crust facilitation of vascular plants may be limited, at least as far as annuals are concerned.

Potential Improvements

Analyzing soil samples from the field plots before carbon was applied and at least a year following application would allow the tracking of nitrogen levels in order to prove that the carbon addition did, indeed, reduce soil fertility. Based on past literature it can be assumed that this would be the case. Soil samples have been collected, but due to funding limitations, they have not yet been analyzed. Another potential improvement to the study would be to include open surfaces in the field experiment. Comparing establishment on open to that on crust and pavement would supplement and further strengthen greenhouse results.
Study Context and Limitations

One limitation of this study involves the quicker carbon breakdown in the greenhouse. Ideally, the carbon source would be reapplied routinely as was done in past experiments that took place in areas of higher rainfall. However, the aim of the greenhouse experiment was to replicate the field experiment, and, due to low rainfall and relatively slow microbial activity, the field experiment only needed a one-time application of carbon. A monthly carbon application, similar to what Reever Morghan and Seastedt (1999) did, would probably produce a stronger response in the greenhouse experiment.

Although *Bromus* density was high across greenhouse experiment flats, there was no significant difference between treatments or surface types. There are a couple of possible explanations for this. First, because the soils were salvaged, the surface types were all slightly disturbed. It could be that instead of measuring *Bromus* establishment by surface type, establishment on disturbed surfaces was really what was being measured. In addition, because it is likely that the carbon had broken down significantly by this time, it is possible that *Bromus* needs higher levels of carbon applied in order to instigate reductions similar to that seen in *Schismus* or *Brassica*.

As is typical with manipulation experiments in the field, variables such as climate, site factors, and species characteristics likely affected the outcomes of the field experiment. While there was enough *Brassica* emergence in the greenhouse for analysis, at the field site there was almost no emergence. This could be due to several different factors involving seed germination. First, studies have found *Brassica* seed to be inhibited by light (Thanos et al. 1991), and seed burial is linked to successful
germination. Because the experiment involved studying relationships of soil surfaces and disturbance, burying seed would have compromised the nature of the study. Therefore, seed was sown on the surface of plots. This probably played a role in its minimal establishment in the field; in the greenhouse, the soil surfaces were slightly disturbed due to the nature of the salvage and the seed could have found better places to wedge itself into.

Light inhibition of *Brassica* seed could have a combined effect with water limitation to further hinder Brassica germination. The second round of seeding at the field site took place in a year with higher than normal rainfall (15.4 cm versus 14 cm), yet germination was almost nonexistent for *Brassica*. It could be that precipitation timing was not optimal, or that it was still not enough to stimulate germination. Documentation of the responses of *Brassica* to water and resources are contradictory and limited. *Brassica* establishment has been linked to high-rainfall years, and it is possible that, while higher than average, rainfall during the study was not high enough to trigger germination in the seed applied. In the wild, *Brassica* can reach maturity and produce seed as early as February, and, plants have usually ended their reproductive cycle by April (Minnich and Sanders 2000). It could be that the timing of the rainfall that occurred was not optimal, as the vast majority of it fell during January and February. The greenhouse experiment seems to support this because there was significantly more *Brassica* germination in the greenhouse under regular irrigation. In addition, field plots were placed in the interspaces between shrubs, avoiding washlets, and it is possible that these locations were not ideal for *Brassica* establishment, especially in moderate rainfall years.
It is also possible that seed was cached by local ant populations. *Brassica* seed is significantly heavier and more substantial than both *Bromus* and *Schismus* seed, and it may have been collected by resident ant populations. There are both ant and rodent mounds present at the site, and, during seeding, extensive ant activity, including granivory, was observed.

**Management Implications**

Reducing soil fertility through the addition of a carbon source is recommended to be used as an alternative to herbicide application. Research into the effects that carbon addition has on native desert plants is necessary, but it is likely that even if it negatively affects them, the repercussions are less severe than those of herbicide application. A cost-benefit analysis should be performed for the use of carbon because the benefits might overshadow any negative consequences. Because more research is needed and biotic impacts have not yet been studied, starting with one small area and monitoring it would be prudent. Based on the experimental results, it seems that, should sucrose be applied on Mojave Desert sites as a carbon source for invasive species mitigation efforts, annual applications would be effective at limiting *Bromus*, *Schismus*, and *Brassica* establishment. Future research on carbon addition in arid environments may recommend the diversification of carbon sources, including both a quick-release source (e.g. sucrose) applied at regular intervals and a slow-release source (e.g. sawdust) applied infrequently. Research into the most effective application frequency and quantity is needed in order to determine the least amount of cost and labor necessary to achieve positive results.

The protection of biological soil crusts and desert pavement is recommended as a means of preventing the further spread of invasive species. Pavements, in particular, had
a strong inhibitory effect on exotic species, and this combined with the large-scale nature of desert pavement, makes pavements physical barriers to invasion. In areas where roads cuts, corridors for invasion, are to be made near desert pavement sites, it is recommended that these roads avoid the pavement as much as possible.

Future Studies

It would be interesting to further examine carbon addition in desert ecosystems such as the Mojave Desert. The practicality of carbon addition as a control technique to be used by land managers relies on three factors: the amount of time that the carbon remains effective in the soil, how much labor is involved in the application, and the quantity and cost of the carbon source. Carbon sources should be further explored in order to discover the most practical and cost-effective sources and methods for land managers. Sawdust and other inexpensive waste products should be compared to sucrose in effectiveness. While sucrose is fast-release, sawdust is slow-release, and the possibility of using these two sources in collaboration should be examined for the desert. The emphasis should be placed on maximizing the length of time carbon stays useful in the soil in order to minimize manual application, cutting down on cost. The rate that these carbon sources break down in the field – with varying levels of rainfall – should be studied in order to determine application timing.

Because the goal is to improve the native ecosystem, studies should be done on the impacts that carbon addition has on native plant species as well as invertebrates, microorganisms, and soil properties. In particular, an experiment of the effects carbon addition has on native species would be useful in determining whether native species are negatively or positively impacted by carbon addition. Past studies in other ecosystems
have shown that natives have benefited from a competitive advantage when carbon was added to decrease exotics (Zinc and Allen 1998; Blumenthal et al. 2003), and a similar experiment could be used to determine whether this is holds true for arid environments.

In order to determine the level of importance that keeping soil surfaces intact plays in limiting invasions, further studies should be performed on early secondary succession in deserts immediately following a disturbance. To do this, exotic establishment should be monitored at routine intervals – perhaps annually – following a disturbance in order to determine what the behavior of these species is in the initial phase following disturbance. Future research should also examine the use of remote sensing for identifying target areas. It is possible that microwaves could be used for aerial classification and detection of large areas of pavement or crust, but future research is needed into the viability of this application. In addition, research should look into whether remote sensing can be used to detect extensive invaded areas in need of remediation. Technology like this could help to prioritize potential target areas.

Acknowledgements

This research was supported through a cooperative agreement between the National Park Service (Lake Mead NRA) and UNLV, coordinated by Alice Newton and Kent Turner of LMNRA. I thank my committee Scott Abella, Wesley Niles, Bill Smith, and Lloyd Stark; Jarrett DeCorte for assistance with fieldwork; Cayenne Engel for help with thesis preparation; and Cheryl Vanier for performing univariate statistical analyses.

Literature Cited


### Tables

**Table 1** Latitude, longitude and elevation for experiment, salvage, and study sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude (°N)</th>
<th>Longitude (°W)</th>
<th>Elevation (m)</th>
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**Table 2** Effects of surface type, carbon addition, and disturbance on *Bromus* density in a field experiment of plant community invasibility in the eastern Mojave Desert. Numerator and denominator degrees of freedom (DF), F-values, and P-values are provided. Minimum adequate model was the full model. P values are bolded if ≤ 0.05.

<table>
<thead>
<tr>
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**Table 3** Effects of surface type, carbon addition, and disturbance on *Bromus* total biomass for the field experiment. Numerator and denominator degrees of freedom (DF), F-values, and P-values are provided. The minimum adequate model included substrate type, carbon addition, and their interaction. P values are bolded if ≤ 0.05.

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Table 4 Effects of surface type, carbon addition, and disturbance on *Schismus* density in a field experiment of plant community invasibility in the eastern Mojave Desert. Numerator and denominator degrees of freedom (DF), F-values, and P-values are provided. Minimum adequate model was the full model. P values are bolded if ≤ 0.05.

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Table 5 Effects of surface type, carbon addition, and disturbance on *Schismus* total biomass in a field experiment of plant community invasibility in the eastern Mojave Desert. Numerator and denominator degrees of freedom (DF), F-values, and P-values are provided. The minimum adequate model included carbon addition. P values are bolded if ≤ 0.05.

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Table 6 Effects of surface type and disturbance on *Schismus* average biomass in a field experiment of plant community invasibility in the eastern Mojave Desert. Numerator and denominator degrees of freedom (DF), F-values, and P-values are provided. The minimum adequate model included only the intercept. P values are bolded if ≤ 0.05.

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Table 7 Analysis of variance for each species analyzing the effects of surface type and carbon addition in a greenhouse experiment of plant community invasibility in the eastern Mojave Desert. P-values were computed from 1000 permutations. P values are bolded if ≤ 0.05.

**Bromus**

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**Schismus**

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**Brassica**

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Table 8 Total vegetative cover ANOVA results in an annual plant community study in the eastern Mojave Desert. The numerator and denominator degrees of freedom (DF) are provided, along with F and P-values. Back-transformed least-squares mean follow, with lower and upper standard errors (SE). Significant differences are denoted by different letters. P values are bolded if ≤ 0.05.

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Table 9 Species richness by surface type ANOVA results in an annual plant community study in the eastern Mojave Desert. The numerator and denominator degrees of freedom (DF) are provided, along with F and P-values. Back-transformed least-squares mean follow, with lower and upper standard errors (SE). Significant differences are denoted by different letters. P values are bolded if ≤ 0.05.

<table>
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Table 10 Proportion of exotics by surface type (ANOVA results) in an annual plant community study in the eastern Mojave Desert. The numerator and denominator degrees of freedom (DF) are provided, along with F and P-values. Back-transformed least-squares mean follow, with lower and upper standard errors (SE). Significant differences are denoted by different letters.

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<td>Pavement</td>
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Table 11 Proportion of forbs by surface type (ANOVA results) in an annual plant community study in the eastern Mojave Desert. The numerator and denominator degrees of freedom (DF) are provided, along with F and P-values. Back-transformed least-squares mean follow, with lower and upper standard errors (SE). Significant differences are denoted.

<table>
<thead>
<tr>
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<th>DenDF</th>
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<th>P-value</th>
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</tr>
<tr>
<td>Pavement</td>
<td>0.23</td>
<td>0.10</td>
<td>0.12</td>
</tr>
</tbody>
</table>
Table 12: Total vegetative cover (ANOVA results) for treatment interactions in an annual plant community survey of a field experiment in the eastern Mojave Desert. The numerator and denominator degrees of freedom (DF) are provided, along with F and P-values. P values are bolded if ≤ 0.05.

<table>
<thead>
<tr>
<th>Effect</th>
<th>NumDF</th>
<th>DenDF</th>
<th>F</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disturbance (Dist)</td>
<td>1</td>
<td>24</td>
<td>2.63</td>
<td>0.1181</td>
</tr>
<tr>
<td>Carbon Addition (C)</td>
<td>1</td>
<td>24</td>
<td>0.00</td>
<td>0.9722</td>
</tr>
<tr>
<td>Surface Type (Type)</td>
<td>1</td>
<td>24</td>
<td>23.31</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Dist*C</td>
<td>1</td>
<td>24</td>
<td>0.32</td>
<td>0.5781</td>
</tr>
<tr>
<td>Dist*Type</td>
<td>1</td>
<td>24</td>
<td>0.18</td>
<td>0.6761</td>
</tr>
<tr>
<td>C*Type</td>
<td>1</td>
<td>24</td>
<td>0.45</td>
<td>0.5095</td>
</tr>
<tr>
<td>Dist<em>C</em>Type</td>
<td>1</td>
<td>24</td>
<td>0.84</td>
<td>0.36</td>
</tr>
</tbody>
</table>

Table 13: Species list for annual community composition survey from four sites across three soil surface types in the eastern Mojave Desert. Cryptantha spp. includes: C. nevadensis, C. barbigera, C. recurvata and Pectocarya sp. includes: P. recurvata, P. platycarpa, P. setosa.

<table>
<thead>
<tr>
<th>Family</th>
<th>Scientific name</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Poaceae</td>
<td><em>Bromus rubens</em> L.</td>
<td>red brome</td>
</tr>
<tr>
<td></td>
<td><em>Schismus</em> spp.</td>
<td>Mediterranean grass</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Chaenactis carphoclinia</em> A. Gray</td>
<td>pincushion flower</td>
</tr>
<tr>
<td></td>
<td><em>Eriophyllum lanatum</em> (Pursh) Forbes</td>
<td>common woolly sunflower</td>
</tr>
<tr>
<td>Boraginaceae</td>
<td><em>Cryptantha</em> spp. (Torr.) Greene</td>
<td>Cryptantha</td>
</tr>
<tr>
<td></td>
<td><em>Pectocarya platycarpa</em> (Munz &amp; I.M. Johnst.) Munz &amp; I.M. Johnst.</td>
<td>broadfruit combsceed</td>
</tr>
<tr>
<td>Brassicaceae</td>
<td><em>Lepidium lasiocarpum</em> Nutt.</td>
<td>shaggyfruit pepperweed</td>
</tr>
<tr>
<td></td>
<td><em>Lesquerella tenella</em> A. Nelson</td>
<td>Moapa bladderpod</td>
</tr>
<tr>
<td>Campanulaceae</td>
<td><em>Nemacladus glanduliferus</em></td>
<td>glandular threadplant</td>
</tr>
<tr>
<td>Plantaginaceae</td>
<td><em>Plantago ovata</em> Forsk.</td>
<td>desert Indianwheat</td>
</tr>
<tr>
<td>Polemoniaceae</td>
<td><em>Gilia</em> spp.</td>
<td><em>Gilia</em></td>
</tr>
<tr>
<td>Polygonaceae</td>
<td><em>Linanthus jonesii</em> (A. Gray) Greene</td>
<td>Jones' linanthus</td>
</tr>
<tr>
<td></td>
<td><em>Chorizanthe brevicornu</em> Torr.</td>
<td>brittle spineflower</td>
</tr>
<tr>
<td></td>
<td><em>Chorizanthe rigida</em> (Torr.) Torr. &amp; A. Gray</td>
<td>devil's spineflower</td>
</tr>
<tr>
<td></td>
<td><em>Eriogonum trichopes</em> Torr.</td>
<td>flatcrown buckwheat</td>
</tr>
</tbody>
</table>
Figure 1 Regional map showing the outline of the Mojave Desert in the southwestern United States. Study sites are in the eastern portion of the region, within Lake Mead NRA, just east of Las Vegas. Map adapted from Abella and Newton (2009).
Figure 2 Map of field experiment site, salvage sites, and community study sites along Northshore Drive within LMNRA. S-1, S-2, and S-3 are the salvage sites for crust, open, and pavement, respectively. F-1 is the field experiment site at Bittersprings Road as well as the community survey site 1. F-2, F-3, and F-4 are the remaining community survey sites. For coordinates, see Table 1.

Figure 3 Field experiment site within LMNRA. Located within a *Larrea-Ambrosia* plant community.
Figure 4 1 m × 1 m desert pavement plot at field experiment site.

Figure 5 1 m × 1 m biological soil crust plot at field experiment site.
Figure 6 1.5 m × 0.67 m biological soil crust plot at field experiment site.
Figure 7 Coverage of *Bromus* and *Schismus* on crust during the first round of data collection at a field experiment site.
Figure 8 Coverage of *Bromus* and *Schismus* on pavement during the first round of data collection at a field experiment site.
Figure 9 Desert pavement salvage site in Lake Mead National Recreation Area.

Figure 10 Biological soil crust salvage site in Lake Mead National Recreation Area.
Figure 11 Open surface salvage site in Lake Mead National Recreation Area.

Figure 12 Procedure for desert pavement salvage.
Figure 13 Salvaged desert pavement, pre-experiment.

Figure 14 Salvaged biological soil crust, pre-experiment.
Figure 15 Salvaged open surface, pre-experiment.

Figure 16 Round 2 greenhouse experiment setup with emergence shown.
Figure 17 Map of community study sites along Northshore Drive within LMNRA. Site 1 is at the Bittersprings Road field study site, Sites 2 and 3 are at Road 100 on gypsum and non-gypsum areas, respectively, and Site 4 is at a pullout between mile 22 and 23. See Table 1 for coordinates.

Figure 18 Surface type by carbon addition for Bromus total biomass in a field experiment of plant community invasibility in the eastern Mojave Desert (+ SE). Letters denote significant differences (P<0.05).
Figure 19 *Bromus* density and biomass based on surface types by carbon and disturbance in a field experiment of plant community invasibility in the eastern Mojave Desert.
**Figure 20** *Schismus* density and biomass based on Surface types by carbon and disturbance in a field experiment of plant community invasibility in the eastern Mojave Desert.
Figure 21 Mean seedlings emerging for *Bromus* across carbon addition treatments, surfaces, and seeded species in a greenhouse experiment of plant community invasibility in the eastern Mojave Desert.
Figure 22 Mean seedlings emerging for *Schismus* across carbon addition treatments, surfaces, and seeded species in a greenhouse experiment of plant community invasibility in the eastern Mojave Desert.
Figure 23 Mean seedlings emerging for *Brassica* across carbon addition treatments, surfaces, and seeded species in a greenhouse experiment of plant community invasibility in the eastern Mojave Desert.
Figure 24 Mean and SE density for *Bromus* across carbon addition and surface types in a greenhouse experiment of plant community invasibility in the eastern Mojave Desert.

Figure 25 Mean and SE density for *Schismus* across carbon addition and surface types in a greenhouse experiment of plant community invasibility in the eastern Mojave Desert.
Figure 26 Mean and SE density for *Brassica* across carbon addition and surface types in a greenhouse experiment of plant community invasibility in the eastern Mojave Desert.

Figure 27 Ordination of relative cover over annual plant community surveys at 4 sites in the eastern Mojave Desert (joint plots cutoff at $r^2=0.20$ for vectors). Vector lengths are proportionate to correlation of species with ordination axes. SCHISPP refers to *Schismus* sp., PLAOVA refers to the native annual forb *Plantago ovata*, and NONE refers to plots were no there was no plant cover.
Figure 28 Ordination of annual plant community composition interactions for disturbance by surface type at the Bittersprings field experiment site in the eastern Mojave Desert (joint plots cutoff at $r^2=0.20$ for vectors). Vector lengths are proportionate to correlation of species with ordination axes. SCHISPP refers to *Schismus* sp., PLAOVAs and CHACAR refer to the native annual forbs *Plantago ovata* and *Chaenactis carphoclinia*, respectively, and NONE refers to plots where there was no plant cover.
Figure 29  Ordination of annual plant community composition interactions for carbon addition by surface type at the Bittersprings field experiment site in the eastern Mojave Desert (joint plots cutoff at $r^2=0.20$ for vectors). Vector lengths are proportionate to correlation of species with ordination axes. SCHISPP refers to Schismus sp., PLAOVA and CHACAR refer to the native annual forbs Plantago ovata and Chaenactis carphoclinia, respectively, and NONE refers to plots were no there was no plant cover.
CHAPTER 4
CONCLUSION

This research examined techniques for limiting future invasions of exotic species in Mojave Desert ecosystems. From these studies, I have drawn these major conclusions:

1. Carbon addition had a species-specific effect on the appearance of exotics, but overall, it reduced establishment.

2. This study has not demonstrated any correlation between disturbance and invasive species establishment although it is only a short-term (two year) study.

3. *Brassica* establishment was almost completely eliminated by carbon addition.

4. *Schismus* showed more limited establishment on pavement than on crust or open surfaces and an overall reduction in establishment following carbon addition.

5. *Bromus* showed significantly less establishment on pavement than crust and, in general, reduced establishment following carbon addition, especially on open surfaces.

6. Desert pavement inhibited establishment of the exotics studied more than crust or open surfaces on average. In a survey of annual plant community composition, pavement surfaces showed lower plant cover and species diversity than crust or open surfaces.

7. Biological soil crusts inhibited establishment of the exotics studied more than open surfaces, and, in a survey of annual plant community composition, crust surfaces showed lower plant cover than open surfaces. Community composition differed significantly for crust surfaces between all sites surveyed.
Based on this research, I identify the following topics in need of additional study:

1. Studies on the effectiveness of different carbon sources in arid environments, including sawdust, wood chips, and sucrose.

2. Studies that explore the success rate of native species compared to exotics when carbon is added in arid environments.

3. Further research on disturbance in relation to exotic species establishment in the desert, especially early recovery.

4. More studies comparing the establishment of exotics and natives on biological soil crusts and desert pavement to open soil surfaces in arid environments.

5. A study of the rate at which the effectiveness of various carbon additions decreases with time, aimed at determining how long land managers can expect carbon addition to remain effective in the soil once it is applied.

6. Research into the viability of using remote sensing to detect large areas of desert pavement and biological soil crust and invaded communities in need of remediation.
VITA

Graduate College
University of Nevada, Las Vegas

Adria DeCorte

Degree:
Bachelor of Science, Architecture, 2005
University of Nevada, Las Vegas

Thesis Title: Relationships of Exotic Plant Invasions with Biological Soil Crust, Desert Pavement, and Soil Carbon in the Eastern Mojave Desert

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