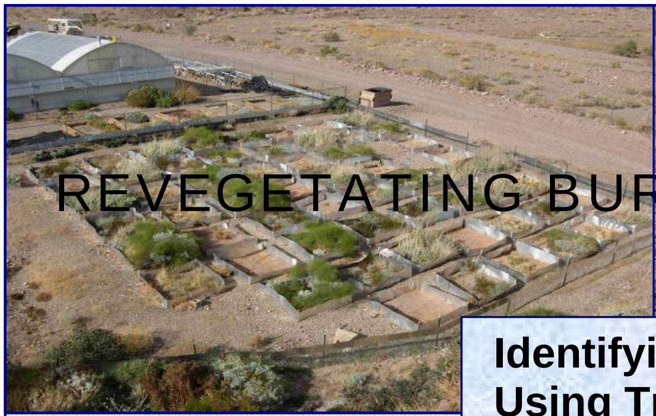

REVEGETATING BURNED ARID LANDS

Identifying Successful Native Species Using Trait and Competition Analysis

Project Title: Revegetating Burned Arid Lands: Identifying Successful Native Species Using Trait and Competition Analysis

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For further information about the Joint Fire Science Program, go to **www.firescience.gov**

I. Abstract

Species selection can make the difference between successful revegetation projects and costly failures. Candidate native species for revegetating burned arid lands in the southwestern United States must meet at least two criteria. These species must: (1) be competitive in post-fire environments typically dominated by exotic grasses, and (2) be able to become established reliably by seeding or planting. In response to Manager's Request Task 3 (reestablishment of native vegetation after fires on arid lands) in the 2006 JFS announcement for proposals, this research tackled the problem of selecting native species with the greatest chance of revegetation success by conducting synergistic experiments and studies in the Mojave Desert. In the first part of the project, we established experimental native plant communities and monocultures of 12 native species ranging from native early successional forbs to late-successional shrubs. We introduced seeds of the invasive, exotic annual grasses *Bromus rubens* (red brome) and *Schismus* spp. (Mediterranean grass) and also manipulated soil nitrogen. We found that an early successional forb community reduced biomass of the exotic grasses by 8- to 33-fold compared to controls (no native vegetation) and below the biomass fire threshold for Mojave Desert ecosystems. Some of these early successional forbs, such as *Sphaeralcea ambigua* (desert globemallow) also performed best in planting trials in the second part of the project, and are recommended species for revegetating desert wildfires. Further work is needed, however, to increase seeding success. In a mensurational field study as the third part of the project, we found that cover of exotic grasses was generally lowest below native perennial species that do not readily form fertile islands, consistent with parts 1 and 2 of the project. In three-value added supplemental parts to the project, we (1) conducted a greenhouse competition experiment of target native species with *Bromus rubens*, (2) conducted a seed fate study with the native species of the project to determine post-seeding seed fates since establishment through seeding on the burn was poor, and (3) a literature synthesis of post-fire responses of native species in the Mojave-Sonoran Deserts, which included the species of this experiment. Collectively, this project's findings have helped identify which native species (e.g., *Sphaeralcea ambigua*) are expected to be most successful for post-fire revegetation efforts and suggest that there is high potential for identifying native species that compete with, and reduce, the exotic annual grasses that fuel fires. These findings are unique, as previous research has focused on the effects of the exotic grasses on native species, and not vice versa.

II. Background and Purpose

Fire was historically rare or nonexistent in most warm desert scrub ecosystems. This has changed, primarily due to the invasion of exotic annual grasses onto desert rangelands (D'Antonio and Vitousek 1992, Brooks 1999). Following wet years, exotic grasses can form a near-continuous cover in the normally open interspaces between shrubs, and can then become highly flammable as standing dead cover during conditions of high air temperatures and low relative humidities that typify dry summer months (Rogers and Vint 1987). Desert fires fueled by these exotic grasses can be intense and cause widespread mortality of native vegetation (Patten and Cave 1984, Rogers and Vint 1987). Furthermore, native desert scrub communities do not readily reestablish after fire (Callison et al. 1985, Brown and Minnich 1986). Often, the exotic grasses that facilitated the fire become even more abundant in the post-burn landscape, frequently achieving virtual monospecific status.

This upsurge of exotic grasses such as *Bromus* spp. initiates a fire cycle that occurs at a greater frequency than the recovery time of the perennial community, predisposing the vegetation to become a fire-controlled annual grassland (Young and Evans 1978, McLaughlin and Bowers 1982). Restoration efforts on post-burn desert landscapes must intervene in this cycle for two reasons. First, it is clear that relying strictly on natural succession leads to community dominance by exotic annual grasses. And second, revegetation efforts with native perennials must limit the competitive advantage of exotic grasses in post-burn successional communities. Candidate native species for revegetation must meet two important criteria in order to be successful in a post-burn landscape. First, they must be able to be established in an open habitat in which "nurse plants" that are so important in recruitment of perennial species in intact desert communities (e.g., McAuliffe 1988) are potentially not available. Secondly, they must persist and compete with exotic grasses that will inevitably be a component of the post-burn plant community. However, few studies in southwestern deserts have examined the competitive effects of native species on the exotics, as most research has focused on the effects of the exotics on natives (e.g., Brooks 2000).

The overall objective of this research was to identify native perennial plants that are competitive with exotic annual grasses and that are amenable to establishing on burns through planting and seeding revgetation methods that land managers could implement. We addressed this objective through an experiment evaluating native vegetation types that best resisted invasion by exotic annual grasses; a correlational field study of the distributions of exotic grasses among native perennials, with a value-added (i.e. supplemental deliverable) greenhouse competition experiment; a planting and seeding study on a desert burn, including a value-added seed-fate study assessing where seeds go once seeded; and a value-added literature synthesis of natural post-fire recovery patterns to identify species with natural tendencies to become established after desert wildfires. Layouts of each of these studies within the overall project are discussed in the following sections.

III. Study Location and Description

The studies occurred in the Mojave Desert in southern Nevada. Descriptions of each project component are provided in the following sections. The first three project components were required per our proposal, while the greenhouse portion of the third part and the last two components are value-added components.

Native vegetation invasibility experiment

This experiment occurred outside and adjacent to the experimental plant nursery within Lake Mead National Recreation Area (LMNRA), in the eastern Mojave Desert, 16 km east of Las Vegas, Nevada, southwestern USA, in *Larrea tridentata-Ambrosia dumosa* vegetation

(36°03'30"N, 114°49'26"W, 381 m in elevation). For the experiment, the previously disturbed site was graded using heavy equipment and an area of 0.05 ha was created for community plots and 0.01 ha for species plots. An enclosure, 1.25 m tall with mesh openings 0.6 cm in diameter and aluminum flashing to a height of 45 cm, was installed around the entire site to discourage herbivory. Community plots, 2 m × 2 m in area, were spaced 0.5 m apart, and 1 m × 1 m species plots were also spaced in rows 0.5 m apart. Soil within plots was excavated to a depth of 0.25 m and replaced with a commercially available sandy loam mixture typical of desert soils (Boulder Sand and Gravel Co., Boulder City, Nevada). These plot soils averaged 76 ± 3% sand (mean ± SD), 12 ± 2% silt, and 12 ± 2% clay (hydrometer method; Burt 2004). A strip of aluminum flashing, 45 cm tall, was installed 20 cm deep into the soil around each plot to further discourage herbivory and reduce interaction between plots.

The community experiment was a three-way, factorial design consisting of native plant community (five levels: early successional forb, shrub, and grass; late-successional shrub; or control with no native plants), exotic species (two levels: *Bromus* or *Schismus* added to plots), and N addition (two levels: added or not), with each of the 20 treatment combinations replicated three times. Three species (all perennial) constituted each of the native plant communities as follows: early forb – *Baileya multiradiata*, *Penstemon bicolor*, and *Sphaeralcea ambigua*; early grass – *Achnatherum hymenoides*, *Aristida purpurea*, and *Sporobolus airoides*; early shrub – *Bebbia juncea*, *Encelia farinosa*, and *Hymenoclea salsola*; and late shrub – *Ambrosia dumosa*, *Eriogonum fasciculatum*, and *Larrea tridentata* (nomenclature follows the PLANTS database, http://plants.usda.gov). The successional classification of species was based on data from 47 studies in the Mojave-Sonoran Deserts using a ratio of disturbed:undisturbed abundance among studies (Abella 2010). The species experiment was a two-way, factorial design including 13 levels of native species (the 12 species from the community experiment each in their own plot and a control with no native vegetation) and two levels of exotic species addition (*Bromus* or *Schismus*), with each of the 26 treatment combinations replicated three times. Treatments were assigned to plots in a completely random design in both experiments.

Native species were grown in 1- or 4-L pots in local greenhouses (LMNRA nursery and the College of Southern Nevada, Henderson, Nevada) from Mojave Desert seed sources for one year before outplanting. In each community plot receiving the native vegetation treatment, 12 individuals of each of the three assigned native species were randomly planted in a 6 × 6 array where one individual of each species was present in each set of three plants. This resulted in a density of 3 plants/m^2 for each species and a total of 9 plants/m^2. In species plots, nine individuals of the assigned species were planted in a 3 × 3 array, also for a density of 9 plants/m^2. In control plots in both experiments, holes were dug and re-filled so that any disturbance associated with planting was constant across all treatment combinations. Native plants were outplanted in plots in December 2008.

Following planting, plots were watered with 0.2 cm/wk of tap water from hoses at the nursery facility to maintain the native plants for the duration of the experiment. A total of 17 cm (83% of average) of natural precipitation fell at the site during the 16-month study period from January 2009 through April 2010. The 73-year average is 14 cm/year based on the Boulder

City, Nevada weather station 10 km away (Western Regional Climate Center, Reno, NV). Seeds of either *Bromus* or *Schismus* were seeded at a density of 100 seeds/m^2 to appropriate plots in both experiments during February 2009 to establish an initial seed bank. Seeds were collected within LMNRA and had a germinability of 50% in pots with soil in greenhouse conditions (daily watering and constant 24^{o}C temperature). A second seeding, using a higher density of 700 seeds/m^2 to provide a propagule pressure that could result in $\geq$ 50 plants/m^2 (the initial seeding of 100 seeds/plot produced 8 plants/m^2), was done in September 2009. Initial applications of N in community plots were performed in February and March 2009, followed by applications in December 2009 and February 2010. Nitrogen was added as NH_4-NO_3 at a rate of 1.7 g N /m^2 to plots in each of the four applications.

Data were collected after the second spring, in May 2010, at the time of peak biomass of annual plants. Aboveground biomass of the exotic grasses was harvested from plots and weighed following oven drying at 60^{o}C for 72 hours. The areal cover of native plants was categorized using 5% cover classes. Samples of the 0-5 cm soil layer were collected from the centers of plots, sieved to 2 mm, and analyzed for NH_4-N (2 *M* KCl extraction, salicylate method), NO_3-N (2 *M* KCl extraction, ion chromatography method), total C and N (dry combustion), organic C (difference between total C and carbonate C), and available P (Olsen method) following Burt (2004). Samples were immediately placed in a chilled cooler and analyzed within 24 hours for NH_4 and NO_3. Foliar samples of native and exotic species were collected from community plots and of native species on species plots (samples of the exotics were collected on controls), ground with a stainless-steel blender, digested with a sulfuric acid-hydrogen peroxide procedure, and analyzed colorimeterically for N and P (Allen 1989).

The response variables of exotic species biomass (transformed as square root) and soil and foliar nutrients were analyzed for both experiments using analysis of variance including all possible factorial interactions with Tukey's test for multiple comparisons in JMP software (SAS Institute 2004). The relationship between the cover of native species and biomass of exotic species was assessed using Pearson and Spearman correlation coefficients.

Burn area planting and seeding species performance experiment

If a species performed well in the first part of the study by competing well with brome, the species still cannot be recommended for revegetation until it is demonstrated that it can reliably become established in a post-fire environment. A field outplanting was undertaken within an area northwest of Goodsprings, NV that had burned in a 2005 wildfire (Goodsprings Fire). The planting area was within a 30 m × 80 m area where ten 80-m long rows were marked and spaced 3 m apart. Planting positions were randomly selected using each meter mark as an option (1-80) for the positioning of 40 plants comprising eight native desert perennials along each row (for a total of 50 plants of each species). Spacing of each plant within rows was at least one meter, but could be two or more meters apart. Additional points were marked for 40 control positions not receiving plants. The eight native perennial species were species from the first part of the project for which we were able to obtain sufficient greenhouse-grown outplants and represented one of four functional groups:

Native desert perennial species for field planting and corresponding functional group category.

Species (with code)	**Functional Group**
Ambrosia dumosa (AMDU)	Late-successional shrub
Eriogonum fasciculatum (ERFA)	Late-successional shrub
Larrea tridentata (LATR)	Late-successional shrub
Encelia farinosa (ENFA)	Early successional shrub
Muhlenbergia porteri (MUPO)	Early successional grass
Sporobolus airoides (SPAI)	Early successional grass
Penstemon bicolor (PEBI)	Early successional forb
Sphaeralcea ambigua (SPAM)	Early successional forb

Plants were grown out and supplied by the Lake Mead NRA nursery, College of Southern Nevada nursery, and the Nevada Division of Forestry nursery from local native seed sources. All of the shrub species and *Sphaeralcea ambigua* were transplanted from 4-L containers, while the two grasses and *Penstemon bicolor* were transplanted from smaller cones from the Lake Mead nursery.

Four treatment levels were randomly assigned to each of the plants and to a blank control. Treatments were selected to test for enhancing the survival of outplanted species. A shelter treatment consisted of enclosing the plant within a green Tubex® tree shelter (a tube ca. 10 cm in diameter and 60 cm tall). These shelters are available through commercial vendors such as Forestry Suppliers, Inc. A water treatment consisted of supplying water in the form of DriWater™ irrigation gel packs (http://www.driwater.com/) that were inserted within plastic tubes planted along side plants and in contact with the rooting zone. These two treatments alone and in combination (i.e. water + shelter) made three of the treatment levels. The fourth treatment level consisted of not supplying the plant with either survival-enhancing technique (i.e. none).

The outplanting occurred in February 2008. A crew of Nevada Conservation Corps members and several Lake Mead NRA nursery staff assisted the UNLV researchers in planting and establishing treatments. Plants were delivered to their randomly assigned positions along with supplies for which treatments they may be given. Holes were dug with shovels and hand trowels and were watered prior to planting with transported tap water. Each month following the outplanting, the site was checked for shelter and DriWater™ status. Shelters often had to be re-anchored around plants since high winds were common. DriWater™ gel packs were replaced every two months in the first year. Plant status was examined for the duration of the project, and we also plan on conducting an additional inventory in spring 2011 after the conclusion of the formal project to obtain 3-year results.

For the seeding portion, four replicate blocks of 20, 1-m^2 plots comprising five plant community types and four treatment combinations were established in January 2008 on the 2005 Goodsprings Fire in the same area as the planting study. Four seeded plant community types (table below) along with a control (no seeded community) were randomly allocated to four possible treatment combinations: 1) caged with supplemental water, 2) cage only, 3) supplemental water only, and 4) no cage or supplemental water.

Seeded species in each native community treatment and the seeding rates used.

Forb community	**Measured seeding rate (Seeds/plot)**	**Actual seeding rate (PLS/plot)[1]**
Baileya multiradiata	500	425
Penstemon bicolor	500	NA
Sphaeralcea ambigua	1000	420
Early shrub community		
Bebbia juncea	500	200
Encelia farinosa	500	210
Hymenoclea salsola	500	338
Grass community*		
Aristida purpurea	500	425
Late shrub community		
Ambrosia dumosa	500	257
Eriogonum fasciculatum	1300	234
Larrea tridentata	500	210

*We were not able to obtain seed of the other species of grass, so we randomly selected non-grass species (*Ambrosia dumosa* and *Sphaeralcea ambigua*) and added seed of these species to keep seeded species richness similar among plots. [1]Based on viability (Tetrazolium) testing information from seed source information; actual rate units are Pure Live Seed (PLS) per plot. Because seeding rates varied, we planned to account for this in the analysis by calculating the percentage of seeds that produced a seedling. However, as shown in the results, no species became established during the study period.

Each 1-m^2 plot was established in one of the four block grids. Each block was a rectangular area of 20 m × 25 m where we positioned four plots each within five rows. Each block was evenly spaced 100 meters apart along a line paralleling an access road. The line was positioned approximately 20 meters north of an access road in an effort to reduce effects from the road but to make access easier. An area of 3 m × 3 m was delineated for each plot within each row and a 2 m buffer was established between each 3 m × 3 m area. The 1-m^2 plots were then centrally positioned within each of the 3 m × 3 m areas to allow for a buffer area totaling 4 m between each plot.

A cage treatment was used to test for (and mitigate) the effects of anticipated herbivory and granivory by mammals known to occur in the area. Wire mesh screening ("hardware cloth") with 1.27-cm^2 mesh was used to construct cages to enclose the 1-m^2 plot. Squares of 1.75 m^2 of the hardware cloth were cut and molded over a 1 m × 1 m × 0.15 m wooden frame to make a cage of similar dimensions (see photo below). Approximately 15 cm of hardware cloth remained around the base of the cage and served primarily as a vertical barrier to animals that may try to burrow down near the wall of the cage.

Constructed cage for seeding experiment

Seeding took place on January 29, 2008. Seeds were hand-broadcast at ground level in the plots and patted down to ensure contact with the ground (especially for light wind-dispersed seeds like *Bebbia juncea*). The weather was cool, calm, and sunny throughout most of the day with a gentle breeze increasing toward the end of the day. We applied 3.8 L of water (tap water from Lake Mead NRA resource management facility) for all the designated water treatment plots on January 31. Supplemental water treatment plots then received 1.9 L of water each month until May. During the experimental setup in January, each plot was examined for baseline species occurrence. From the baseline plant assessment, the most common species throughout the burned area was the non-native annual, *Erodium cicutarium.* Other seedling species observed both in and around the plot areas were *Sphaeralcea ambigua*, *Astragalus* spp., *Baileya multiradiata*, *Ambrosia dumosa*, *Eriogonum inflatum*, and one *Larrea tridentata* seedling. The non-native annual grass *Bromus rubens* was present but sparse and generally was absent from many of the plots. *Erodium cicutarium* was the dominant ground cover. Few species were found within plots; however, plots with species used in seeding were noted in order to not count them during later assessments. Plots were assessed in May for germination, but no new seedlings were observed.

Watering was halted during the summer since no germination had occurred. In October, watering recommenced at the same rate (1.9L/month). However, in December 2008, much of the area was blanketed in snow with depths approaching 15 cm and no water was applied. The precipitation for the study area is reported below:

Precipitation recorded within 3 km of the seeding study site at the "Goodsprings 2" weather station monitored by the Clark County Regional Flood Control District.

Month Year	**"Goodsprings 2" Precipitation (cm)**	**Normal precipitation for Clark County, NV (cm)**
January 2008	**2.9**	1.49
February 2008	**2.6**	1.75
March 2008	0.1	1.49
April 2008	0	0.38
May 2008	0.3	0.61
June 2008	0	0.20
July 2008	**1.9**	1.11
August 2008	0.5	1.14
September 2008	0.2	0.79
October 2008	0	0.61
November 2008	**1.0**	0.79
December 2008	**2.1**	1.02
January 2009	0.3	1.49
February 2009	**3.4**	1.75
March 2009	0.2	1.49

Overall, annual precipitation in the study area was approximately average or slightly above for the time periods reported based on long-term averages for Clark County, NV.

During the next two seasons, plots were re-assessed for new seedlings, but none were found by the end of the study period. We plan to conduct an additional assessment in spring 2011 after the formal end of the JFSP project.

Given that propagule pressure from native seeds was extremely high and seasonal moisture levels should have been adequate, the lack of response was unexpected given that seeding has show success in some instances in the Mojave Desert (Abella and Newton 2009).

Field and competition assessment of exotic grasses among native perennial plants

We conducted two assessments: one was related to distributions of exotic grasses among native perennial plants in the context of desert roadsides, and another in the context competition between the exotic *Bromus rubens* and native species. The roadside assessment is published (Craig, D.J., J.E. Craig, S.R. Abella, and C.H. Vanier. 2010. Factors affecting exotic annual plant cover and richness along roadsides in the eastern Mojave Desert, USA. Journal of Arid Environments 74:702-707). The second correlational field assessment and competition work is in press in the journal Invasive *Plant Science and Management*, and is described below including the greenhouse competition.

Study Area

Our work focused on species inhabiting the Mojave Desert, a 124,000-km^2 hot desert of southeastern California, southern Nevada, southwestern Utah, and western Arizona in the southwestern USA (Rundel and Gibson 1996). A weather station (Las Vegas, NV, elevation 662 m) typifying the eastern Mojave Desert has reported averages of 11 cm yr^{-1} of precipitation, July daily maximum temperature of 40^oC, and January daily minimum temperature of 1^oC (1937 to 2009 records; Western Regional Climate Center, Reno, NV). This desert receives > 60% of its rainfall in winter, facilitating peak biomass of both native and exotic annual plants in late spring (March through May) during moist years (Beatley 1974). Seedlings of many native perennials also germinate during this period, with growth of the seedlings and mature plants occurring primarily during the warm spring and summer months (Turner and Randall 1987). The typical physiognomy of the desert is widely spaced native perennial plants, such as *Larrea tridentata* and white bursage (*Ambrosia dumosa* (A. Gray) Payne), with interspaces between the shrubs containing annual plants (in moist years) or sparsely vegetated soil.

Competitive Hierarchy Experiment

Following Keddy et al. (2002) for developing competitive hierarchies, we selected 35 species native to the Mojave Desert that ranged widely in growth form (16 annual forbs, 3 perennial grasses, 7 perennial forb-subshrubs, and 9 perennial shrubs), longevity (16 annuals and 19 perennials), and successional affiliation based on Abella (2010). Nomenclature and growth form and longevity classification follow NRCS (2010). We obtained seed[1,2] of the native species from the plant nurseries of Lake Mead National Recreation and the Las Vegas Springs Preserve, both within the Mojave Desert. We collected *Bromus* seed from two populations within Lake Mead National Recreation Area. We conducted a pilot emergence assay (one month duration, with 20 seeds sown in one 3.8-L pot per species with the same soil to be used in the experiment) to determine seed emergence rates to estimate the number of seeds needed to be sown to produce the desired density for the competition experiment.

Based on the emergence information, we sowed seeds of native species for the competition experiment in separate pots to attain a density of 5 seedlings per pot (278 m^{-2}). We simultaneously sowed seeds of the *Bromus* phytometer in the same pots containing the native species to also attain a density of 5 seedlings per pot for *Bromus*. Due to the large number of species tested, we were only able to assess a single density. This density, however, is within the range reported for Mojave Desert field sites in years that have precipitation patterns supporting *Bromus* growth (Beatley 1966; Hunter 1991). To try and ensure close contact of natives with *Bromus*, we used 3.8-L pots that were circular with a diameter of 15 cm. We filled pots with a sterile soil mix consisting of 2:1 sand:potting soil[3] to simulate the sandy loam textures within ranges commonly characterizing Mojave Desert soils (Lato 2006). Our target was to have three replicate pots for each native species, so we sowed seeds in four pots in case some pots lacked sufficient seed germination to attain the target density. We also grew 5 seedlings per pot of brome alone in 10 replicate pots. We randomly arranged pots on a bench in a greenhouse maintained at 24^oC without supplemental lighting. Pots were watered with a misting system in operation for two minutes each day that delivered 1.5 cm of water per day.

We initiated the experiment in April 2009, when *Bromus* actively grows in the field (Beatley 1966), and ran the experiment for eight weeks. Each week, we measured the heights of native and *Bromus* plants and counted the number of plants per pot, thinning plants to the target density of 5 plants per pot as needed. At the end of the experiment, which was the time of senescence of *Bromus* and the native annuals, we harvested above- and below-ground biomass by species within pots and determined oven-dry weight by heating at 70^{o}C for 24 h. Because we averaged data from all plants by species within pots, distinguishing root masses (which could become intertwined by growing in close contact) of individual plants within species was not necessary.

Despite the pilot study and oversowing many species, eight species failed to attain the target density in at least three replicate pots and were not further included in the experiment. While it is possible that manipulating seeds could have increased germination and emergence, we chose to minimally manipulate seeds and avoid attempting species-specific treatments that could have confounded among-species comparisons of competitive abilities. For example, gibberellic acid may have enhanced germination of some species, but this treatment can affect subsequent seedling growth (Baskin and Baskin 2001). A total of 27 species, 12 annuals and 15 perennials, had sufficient emergence for inclusion in the experiment.

Field Patterns of *Bromus* below Native Perennials

We used seven sites, located in Lake Mead National Recreation Area, Red Rock Canyon National Conservation Area, and surrounding Bureau of Land Management land in southern Nevada in the eastern Mojave Desert, to assess the cover of *Bromus* below native perennial species. We selected these sites because they contained a variety of perennial species to permit within-site comparisons and harbored some of the species included in the competition experiment. These sites also contained *Bromus* infestations, which we identified based on a landscape-scale assessment of invasive species distributions in the study area (Abella et al. 2009b). Elevations of the sites ranged from 710 to 1,367 m. The sites were in the 421, 731, 732, and 750 mapping units of the Clark County soil survey and were primarily classified as loamy-skeletal, carbonatic, mesic, shallow Calcic Petrocalcids and Typic and Lithic Torriorthents (Lato 2006). These soils have gravelly loam and sandy loam textures (Lato 2006). Sites had a geographic extent of 64 km, spanning the Universal Transverse Mercator coordinates of 642,316 m E, 4,001,353 m N and 702,253 m E, 3,981,227 m N (zone 11, North American Datum 1983).

At the center of each site within an area of 1 ha, we established four belt transects (one in each of the cardinal directions) that were 5 m wide and up to 50 m long. Along each transect, we measured the first two individuals of any perennial species intended to be included in the competition experiment. We required that an individual have a developed canopy (which excluded sampling seedlings of these species) that did not overlap with the canopy of any other perennial species. We measured the perimeter of each individual canopy (at its greatest extent) and calculated canopy area from perimeter using the formula for a circle to approximate the shape of the canopies. In a vertical plane to the ground below canopies, we visually categorized areal cover of *Bromus* below each perennial plant using the following cover classes: 0 = 0% cover, 1 = > 0 < 1%, 2 = 1 to 3%, 3 = 3 to 6%, 4 = 6 to 12%, 5 = 12 to 25%, 6 = 25 to 50%, 7 = 50 to 75%, and 8 = 75 to 100%. Two interspaces (defined as an area ≥ 1 m from the nearest perennial plant canopy) were also identified using random coordinates within each transect and sampled in the same manner. The dimensions to be sampled within the interspaces were determined based on the dimensions of two randomly selected perennials measured in transects. *Bromus* was the predominant standing annual at all sites, although at one site small amounts of the exotic annual grasses *Schismus* spp. and cheatgrass (*Bromus tectorum* L.) were intermingled with the *Bromus* stalks. These species were included in the *Bromus* cover estimates, as the mat of plant matter at this site was difficult to partition into the small amounts of the other species. Because of *Bromus*'s contribution to hazardous fuels, standing dead biomass is as important as green biomass. We made measurements from November 2009 to January 2010 when *Bromus* was not actively growing and sampled standing dead biomass as a measure of recent accumulated biomass. Dead *Bromus* plants can persist for more than two years (Beatley 1966).

Data Analysis

For the competition experiment, we calculated native species performance versus *Bromus* as the percent of grown-alone biomass that *Bromus* attained when grown with a native species (Equation 1).

(*Bromus* biomass when grown with a native species/*Bromus* grown-alone biomass) × 100 [1]

Because data did not meet assumptions of homogeneity of variance and normality, we compared performance among species using a nonparametric Kruskal-Wallis test followed by Tukey's test ($\alpha = 0.05$) for multiple comparisons in SAS software (PROC NPAR1WAY, followed by PROC MIXED on the ranks; SAS Institute 1999). Because the original data were continuous, we report means and standard errors of the means for interpretive purposes but present the nonparametric statistical results. We used Pearson correlation coefficients, as Spearman rank coefficients were similar, to examine relationships among *Bromus* and native species traits. Traits included root and shoot length, and root, shoot, and total biomass for mono-specific and mixed-species pots. All values in the experiment were averaged on a pot basis and expressed as averages per plant, and were further averaged on a native species basis for analyses at the among-species level.

Despite selecting mixed-species sites for the field study, no site contained all of the species that were included in the competition experiment and species composition of the sites was not identical. Because of this, we viewed the sites and transects as frameworks in which to sample within a defined area, and each perennial plant as a discrete individual unit for analysis. In a non-parametric analysis to accommodate the categorical cover data, we compared the median percent cover (based on midpoints of cover classes) among perennial species and interspaces with a Kruskal-Wallis test followed by Tukey's test for multiple comparisons (SAS Institute 1999). Confidence intervals at the 95% level were computed through the PROC UNIVARIATE and CIQUANTDF option routine.

Post-fire seed fate of native species

This project was a value-added component to our overall project. Because seeding was not successful, we wanted to know what was happening to the seeds. Therefore, we conducted a supplemental seed removal experiment described below.

Experimental design

We used a total of 84 cages in a randomized complete block design nested within burned and unburned habitats to quantify seed removal and seedling emergence. Three experimental treatments were created to allow access to seeds either by: 1) ants only, 2) rodents only, and 3) neither ants nor rodents (control). We used hardware cloth (1.27 cm mesh size) to construct three different cage types that allowed or denied seed consumers access to experimental seeds. Each cage was cylindrical in shape, approximately 30 cm high and 45 cm in diameter, and buried to a depth of approximately 10 cm to prevent rodent access by digging under cages. Ant cages excluded access to rodents, but allowed ant seed removal. Rodent cages had 4 holes (6 cm × 6 cm) cut in each side to allow small mammal seed removal and a piece of vinyl flashing around the cage coated with Fluon (BioQuip, CA, USA) denied ant access to seeds. Fluon was brushed onto a 2 cm exposed area which created a slippery surface and prevented ants from obtaining a foothold on the treated area. Control cages excluded all seed consumers (no holes were cut, and vinyl flashing coated with Fluon denied ant access to seeds). Cages had a top, hence excluding seed removal by birds. Cages were set up in six blocks in burned and unburned habitats at 15 m intervals from each cage and block. Seed removal and germination treatments were randomly assigned within blocks. All treatment combinations were replicated once within each block.

Seed removal experiments

In 2008 and 2009 over a 12-month study period, we used seed removal experiments to estimate relative levels of seed predation. Seed removal trials were conducted at monthly intervals, starting in October 2008 and ending in October 2009. Seed removal trials were not conducted in December 2008 due to snow cover at the study site. During seed removal trials, we used seeds of nine native species varying in size and mass. Seeds were obtained from the U.S. Bureau of Land Management (Southern Nevada District, Las Vegas, Nevada) and had been used in direct seeding of burned habitats. When used for direct seeding, seeds were aerially broadcast at a rate typically ranging between 1 to 70 seeds /m^2. In each cage, a Petri dish (120 × 15 mm) containing 20 seeds of each species (180 seeds) was set up, and seeds were offered for 4 nights. During Petri dish collection, we used masking tape to secure the lids of Petri dishes to prevent seed spillage while seeds were being transported to the laboratory. The amount of seed removed was quantified by subtracting the number of seeds removed from the original number of seeds offered. Handling of seeds was performed with long point tweezers to eliminate confounding factors (e.g. human scent) that may bias seed removal rates (Duncan et al. 2002).

Seed attributes

Seed measurements included mass and length along the greatest axis. By averaging measurements of 20 seeds per species, mass was determined using an analytical balance (Sartorius, New York, USA) and length using digital calipers (Mitutoyo, Chicago, USA).

Seedling recruitment

Starting in November 2008, we sowed 20 seeds per species in cages that allowed or denied seed consumers access to seeds to address the effects of seed consumers on seedling recruitment and establishment of the nine native species. Seed consumer treatments included a rodent and ant access cage (both access), in addition to treatments used in the seed removal study (see experimental design). We inventoried cages for seedling emergence at monthly intervals, and emerged seedlings of sown species were tagged and counted. Tagged individuals were followed through time to evaluate granivory and habitat effects on seedling survival.

Data analysis

Seed removal for each seed species was modeled as a partially hierarchical design in an analysis of variance (ANOVA) that included experimental block as the subject effect, burned and unburned habitats as the between-subject effects, and seed removal treatment and date as within-subject effects. The arcsin-square root-transformed proportion of seeds removed by seed consumers in each seed removal trial was used as the dependent variable. The data transformation improved homoscedasticity and normality. Multiple comparisons were made using a Bonferroni adjustment for all habitat and treatment combinations within dates. Statistically significant differences in seed removal were considered if $p < 0.05$. Analyses were conducted in SAS v. 9.1 (SAS Institute 1999).

Seed attributes such as mass and size influence seed removal patterns (Brown and Leiberman 1973, Price 1983, Crist and MacMahon 1992); therefore, we evaluated effects of these attributes on seed removal. The relationship between seed mass or size and the probability of seed removal was modeled using ordinary least squares regression. All variables were $\log_{10}$ transformed to meet assumptions of normality prior to analysis, and 95% confidence intervals were created from 1000 permutations (Legendre and Legendre 1998). We examined relationships graphically because in some cases large seeds were highly influential on regressions, and slopes which did not include zeros in their 95% confidence interval had a significant impact on proportion of seed removed. The analysis was implemented in R 2.10.1 (R Development Core Team 2009) using the ‘lmodel2’ package.

Effects of burned and unburned habitats and seed removal treatment on proportion of seedling recruitment were evaluated using a generalized linear model with binomial error term. In the model, experimental blocks were the subject effect, habitat condition (burned or unburned) was the between-subject effect, and seed removal treatment (ant and rodent) and their interaction were modeled as within-subject effects. Mean values were back-transformed prior to reporting, and multiple comparisons were Tukey adjusted. Comparisons were only considered when the ANOVA p-value was significant (main effect $p < 0.05$ and interaction term $p < 0.10$). The model was fit in SAS v9.1 Proc Glimmix (SAS Institute 1999). Seedling survival probabilities among habitat type and granivory treatments on censored data were estimated using the Cox proportional hazard regression model. The analysis was conducted in R 2.10.1 using the survival package (R Development Core Team 2009).

Literature review of native species post-fire responses

We conducted a supplemental systematic review of the literature to synthesize knowledge on the natural post-fire responses of desert perennials, including those of our studies. Methods for this review are below:

Literature search

Literature was obtained in 2008 using a reproducible procedure consisting of: (1) searching the article databases of Agricola (covers the 1500s to the present), Biological Abstracts (1969-present), JSTOR (covers individual journals since their inception up to 2005-2006), and Google Scholar (http://scholar.google.com/; all years) using combinations of the key words succession, disturbance, fire, recovery, change, Mojave, and Sonoran in the article title and key words; (2) examining reference lists in located papers; (3) searching other reviews of Mojave and Sonoran Desert vegetation including Humphrey (1963), Brooks and Minnich (2006), Keeler-Wolf (2007), Schoenherr and Burk (2007), and desert species in the U.S. Forest Service Fire Effects Information System (http://www.fs.fed.us/database/feis/); and (4) running a cross-reference search in Google Scholar to examine papers that cited articles located by procedures 1-3. To qualify for inclusion in the analysis, studies had to meet the following criteria: monitor vegetation after wildfire or prescribed fire in the Mojave or Sonoran Desert, report quantitative data on post-fire sprouting or plant community composition, and include data on unburned areas for comparison with burned areas. Because most studies reported data on perennial rather than annual composition, the analysis included only studies of perennials based on the Natural Resources Conservation Service (NRCS; 2010) classification of longevity. Only published data were included, except for Abella et al. (2009a) for which we had access to full community data.

Data analysis

For assessing sprouting frequency, we constructed a study × species matrix of sprouting percentages. We used simple linear regression to examine the relationship of TSF and perennial cover within studies. We averaged cover within studies that reported data from multiple fires of the same TSF, and we did not include cover of *Agropyron* spp. in Callison et al.'s (1985) study since these species were seeded. To analyze literature reporting community data, we extracted the data from the original publication, updated species nomenclature to NRCS (2010), and computed a relative measure of abundance for each species in each study. Relative abundance was computed as the proportion a given species contributed to the total abundance of all species in a sampling unit (plot, transect, or site) within a study (McCune and Grace 2002). This measure was expressed as a percentage summing to 100% on a sampling unit basis when all species were included. We used this relative measure to standardize abundance because studies reported plant cover, density, or frequency, and this standardization also permitted the isolation of community composition from total community abundance. To explore changes in post-fire species composition through time, we computed a Sørensen similarity index (McCune and Grace 2002) of burned:unburned species composition (based on relative abundance) and regressed TSF with this index within studies. We also computed a similarity matrix comparing burned sampling units for each TSF within studies to analyze trajectories in burned composition. We analyzed patterns in individual species by calculating a ratio of burned:unburned relative abundance based on mean relative abundance in all community studies. Species abundances were averaged across fires within a study if that study examined multiple fires.

To examine variation in community composition between the Mojave and Sonoran Deserts, composition was averaged on a study basis separately for burned and unburned areas. We used non-metric multidimensional scaling (NMS; autopilot thorough setting) in the software PC-ORD (McCune and Mefford 1999) to ordinate burned and unburned species composition. To isolate the relative difference between burned and unburned composition, we further ordinated burned composition using unburned composition as a covariate using the NMS successional vector subroutine.

IV. Key Findings

Native vegetation invasibility experiment

Understanding factors influencing exotic species invasions within indigenous ecosystems is critical for reducing damage by exotic species. By assembling experimental native plant communities ranging from early successional forbs to late-successional shrubs and monocultures of 12 native species, we examined the influences of resident perennial vegetation and soil N on the establishment of two exotic annual grasses (*Bromus rubens* and *Schismus* spp.) at a Mojave Desert field site. *Bromus* was more invasive and produced greater biomass than *Schismus*. Compared to early successional grass and shrub and late-successional shrub communities, an early forb community best resisted invasion, reducing exotic species biomass by 8- (N added) and 33-fold (no N added) below amounts in controls (no native plants). However, the least invaded early forb community did not reduce soil N or P relative to other communities, although N addition increased exotic establishment overall. In native species monocultures, *Sphaeralcea ambigua*, an early successional forb, was the least invasible monoculture, reducing exotic biomass by 11-fold below controls. This study provides the first experimental field evidence that native vegetation types may exist that can reduce exotic grass establishment in the Mojave Desert, with early successional native forbs apparently more effective than mid- or late-successional shrubs.

Burn area planting and seeding species performance experiment

The highest mortality rate among all of the plants occurred within the first 45 days and gradually lessoned (but still occurred) beyond 90 days. Many of the plants transplanted from small cones suffered high early mortality while plants transplanted from 4-L containers generally suffered less. In the first 45 days, all *Sphaeralcea ambigua* survived and nearly 90% of *Eriogonum fasciculatum* and *Larrea tridentata* remained alive. *Ambrosia dumosa* suffered over 25% mortality while all other species suffered between 60 and 95% mortality.

Water and shelter treatments, especially when combined, generally improved survival for most plants. Between the status check on day 220 and day 360, no further mortalities were observed. In fact, some plants thought to have died, were later recorded as live. Survival ranged from 9% in controls to 28% in water + shelter. What we believe is especially noteworthy, however, is the fact that species such as *Sphaeralcea ambigua* exhibited high survival (50%) without treatment and very high survival for (70-80%, especially for deserts) in the water and water + shelter treatments. These findings suggest that planting is feasible for burn revegetation in the desert given careful species selection and given strategic planting arrangements such as for creating revegetated island seed sources with limited dollars available for planting. Final data from the study period are below:

Survival data among plants and treatment levels for the outplanting study near Goodsprings, NV. Numbers represent the numbers of plants (40 for each species and 100 for each treatment) with survival percentages at the bottom and far right.

Treatment	**SPAM**	**ERFA**	**LATR**	**AMDU**	**ENFA**	**MUPO**	**PEBI**	**SPAI**	**%**
none	5	2	0	2	0	0	0	0	9
shelter	6	2	2	4	0	0	0	0	14
water	8	6	4	1	2	0	0	0	21
water + shelter	7	7	6	4	0	2	1	1	28
Total	26	17	12	11	2	2	1	1	
Percent survival	65%	43%	30%	28%	5%	5%	3%	3%	

Ambrosia dumosa (AMDU), *Eriogonum fasciculatum* (ERFA), *Larrea tridentata* (LATR), *Encelia farinosa* (ENFA), *Muhlenbergia porteri* (MUPO), *Sporobolus airoides* (SPAI), *Penstemon bicolor* (PEBI), *Sphaeralcea ambigua* (SPAM)

As mentioned in the study description, no seedlings of seeded species were observed on seeded plots. We anticipate continuing to collect data on these plots.

Field and competition assessment of exotic grasses among native perennial plants

The interactions between native and exotic species occur on a continuum from facilitative to competitive. A growing thrust in invasive species science is differentiating where particular native species occur along this continuum, with practical implications for identifying species that might reduce the invasibility of ecosystems. We used a greenhouse experiment to develop a competitive hierarchy of 27 native species with red brome (*Bromus rubens*), an invasive annual grass in southwestern USA arid lands, and a field study to assess *in situ* responses of brome to native perennial species in the Mojave Desert. Native species most competitive with brome in the competition experiment included the annuals pincushion

(*Chaenactis stevioides*) and bristly fiddleneck (*Amsinckia tessellata*) and the perennials eastern Mojave buckwheat (*Eriogonum fasciculatum*), sweetbush (*Bebbia juncea*), and brittlebush (*Encelia farinosa*) that reduced brome biomass to 49 to 70% of its grown-alone amount. There was no clear difference in competitive abilities with brome between annual and perennial natives, and competiveness was not strongly correlated ($r = 0.15$) with the biomass of native species. In the field, sweetbush and brittlebush supported among the least cover of brome, suggesting congruence of the strong early competitive abilities of these species with *in situ* patterns of brome distribution. At the other extreme, brome attained its highest average cover (19%) below littleleaf ratany (*Krameria erecta*), significantly greater than all but three of the 16 species evaluated. Cover of brome was only weakly related ($r = 0.19$) to area of the perennial canopy, suggesting that factors other than the sizes of perennial plants were linked to differences in brome cover among species. Results suggest that (i) interactions with brome differ substantially among native species, (ii) these interactions are not as closely linked to biomass production as in more temperate regions, and (iii) there is potential for identifying native species that can reduce invasion of desert ecosystems.

Post-fire seed fate of native species

In desert ecosystems, selective foraging by seed consumers affects distributions of soil seed banks and consequently plant community composition. However, in burned habitats where direct seeding is used to restore depleted soil seed banks, the roles of seed harvesters in influencing seeding success have not been assessed. We evaluated patterns of seed removal of nine seeded species over 12 months in burned and unburned creosote bush (*Larrea tridentata*) scrub in the Mojave Desert of southern Nevada, USA. Seed removal patterns were influenced by season, habitat condition, and seed species. Proportion of seed removed was highest during spring and summer, presumably because foraging activity of seed consumers increased during warm weather. Rodents removed the greatest amount of large seeds of *Coleogyne ramosissima* in burned and unburned habitats while ants removed the greatest amount of small-seeded species (*Penstemon bicolor, Encelia farinosa,* and *Sphaeralcea ambigua)* in unburned habitat. Seed removal imposes limitations on seed availability, particularly for large seeded-species. Protecting seeds from seed consumers significantly increased seedling establishment. By selectively harvesting preferred seeds granivorous rodents and ants may hamper reseeding efforts intended to restore soil seed banks depleted by wildfires. Direct seeding may be a viable strategy for seed reintroduction if seeds are protected from granivory. Moreover, to reduce loss of seeds to seed consumers foraging activity, site condition and species selection need to be considered when planning direct seeding projects.

Literature review of native species post-fire responses

Increasing wildfire activity is one of the most pressing management concerns in arid lands of the American West. To examine post-fire recovery of perennial vegetation in the Mojave and Sonoran Deserts, I analyzed data systematically synthesized from the literature. Post-fire sprouting by desert perennials is generally limited but varies among species. For example, only 3-37% of *Larrea tridentata* sprouted compared to 64-86% of *Yucca schidigera*. Four of five studies measuring recovery of perennial cover reported close relationships ($r^2 = 0.67$-0.99) between time since fire (TSF) and cover. In fact, three studies measuring the longest TSF (≥ 37 years) found that cover had returned to within 10% cover of unburned areas within approximately 40 years. Conversely, post-fire species composition exhibited little convergence with unburned composition in five of six studies even 47 years after fire. *Sphaeralcea ambigua*, *Gutierrezia* spp., *Achnatherum speciosum*, *Encelia* spp., *Hymenoclea salsola*, and *Baileya multiradiata* had the highest burned:unburned abundance ratios, although overall post-fire community composition differed between the Mojave and Sonoran Deserts. Analyzing the literature as a whole suggested some generalities (e.g., that perennial cover reestablishes faster than composition), but more work is required for improving specific knowledge about plant recovery among fires, sites, species, and climates.

V. Management Implications

Based on these studies, we identify the following overall management implications:

- There is great potential for identifying native species that can compete with exotic annual grasses and that are amenable for revegetating desert wildfires. We suggest that overall, early successional native species have the most potential for competing with exotic grasses in the short- and long-term. In the long-term, later successional perennials often form fertile islands that facilitate exotic species invasions.

- The early successional species that we recommend are species such as *Sphaeralcea ambigua* (globemallow) and *Penstemon bicolor* (pinto beardtongue). While not all early successional species performed well, this group of species appears to have the greatest potential to compete with exotic annuals.

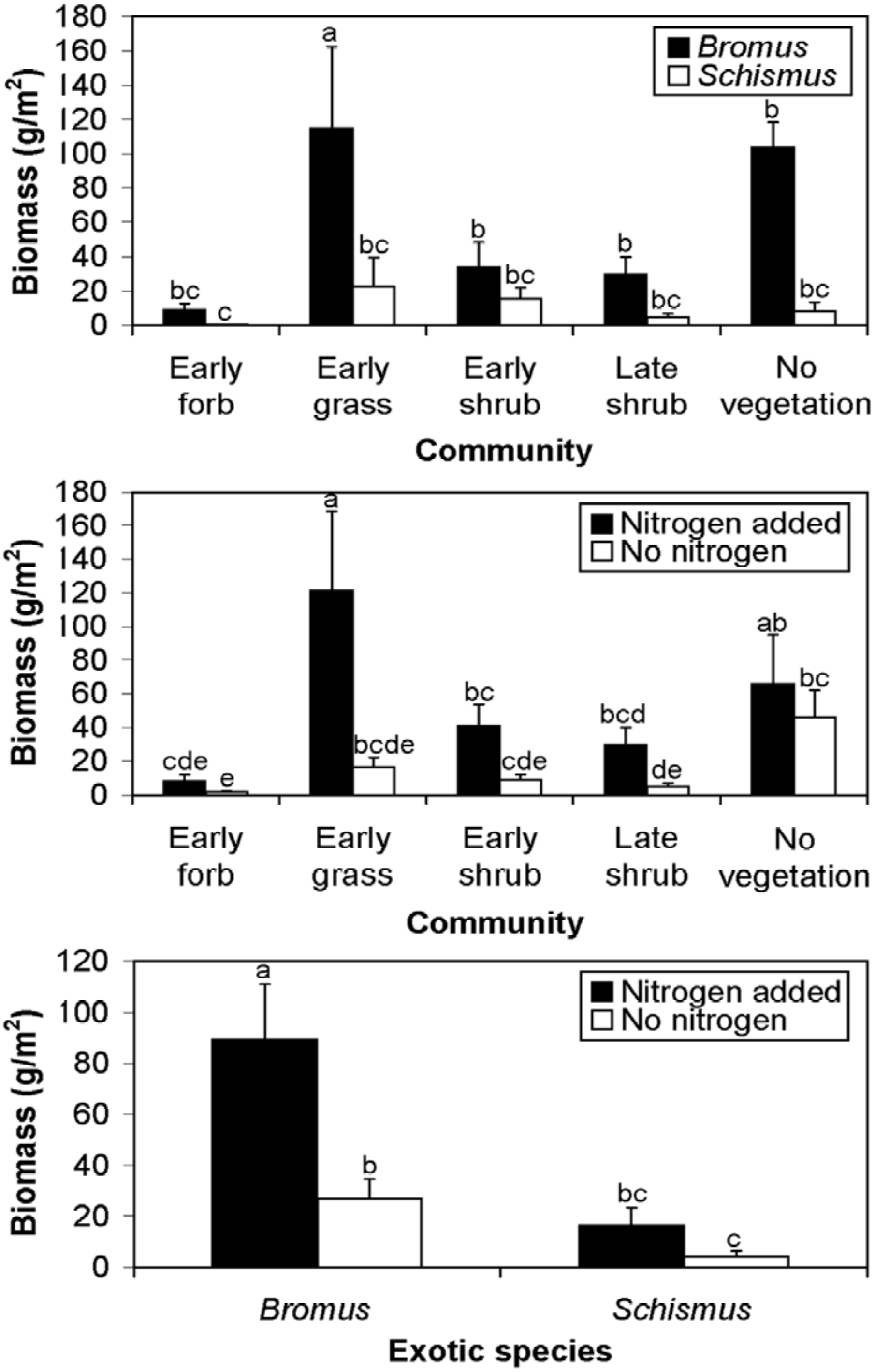
- Encouragingly, an early successional forb community resisted invasion by the exotics even under high levels of soil nitrogen simulating anthropogenic nitrogen deposition.

- Our planting and seed-fate studies suggested that protecting planted seedlings (e.g., through shelters) and seeds from seed-eating organisms may be needed to enhance revegetation success. The seed-fate study indicated that seeding in fall/early winter (October-November) just before germination occurs (in moist years) might best protect seedlings from granivores.

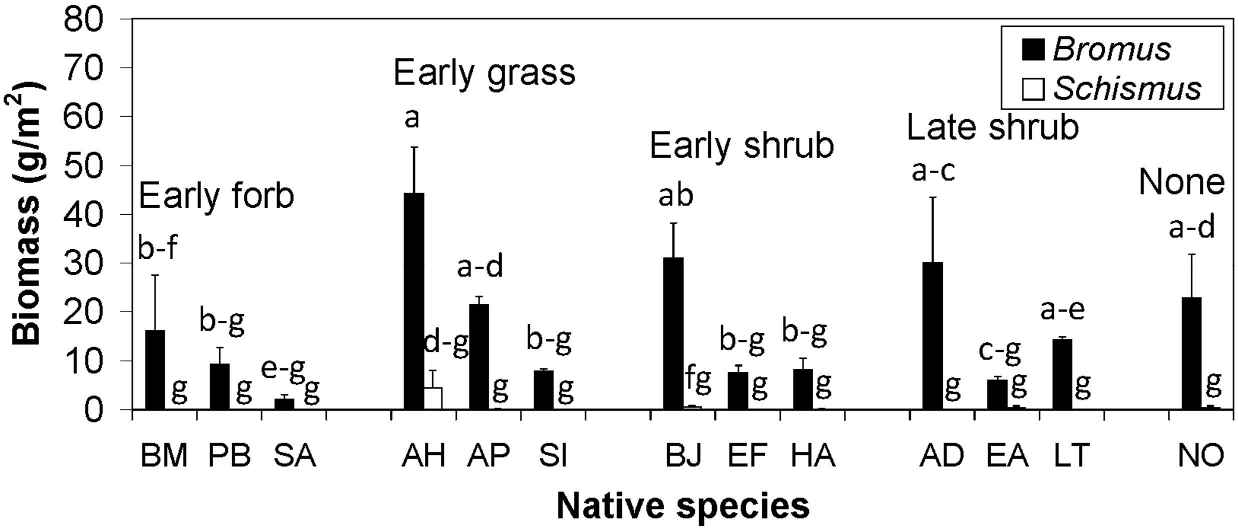
- This research provides the first experimental field evidence that native species exist in the Mojave Desert that can compete with exotic annual grasses which are fueling fires in southwestern deserts. The challenge from here is to develop procedures that can increase the establishment rates of these competitive natives, and to evaluate factors such as the minimum densities of the natives that managers would have to get established to reduce exotic fuel loads below fire thresholds.

- Significantly, the species (*Sphaeralcea ambigua*; globemallow) most competitive with exotic annual grasses in the invasibility portion of our research also performed extremely well in outplanting trials on a 2005 burn. Survival of globemallow was 50% without any kind of treatment. Unfortunately, seeding was not successful. Identifying methods for improving seeding success of this (and similar) species through future research would represent major progress in the revegetation of burned desert lands.

- Some of the major results are summarized graphically and in tabular form on the following pages:



Responses of exotic species biomass to the experimental factors of constructed native community type and N addition in the Mojave Desert, in the community experiment as part of the first part of our project. Top: native community type × exotic species (*Bromus rubens* or *Schismus* spp.); middle: native community type × soil N addition; bottom: exotic species × N addition. Error bars are standard errors of the means. Means without shared letters within an interaction differ at *P* < 0.05 (Tukey's test).



Effects of individual native perennial species on exotic species biomass in the Mojave Desert, USA. Error bars are standard errors of the means. Means without shared letters within an interaction differ at *P* < 0.05 (Tukey's test). Native species are organized by successional stage (e.g., early forb) and are abbreviated as: BM = *Baileya multiradiata*, PB = *Penstemon bicolor*, SA = *Sphaeralcea ambigua*, AH = *Achnatherum hymenoides*, AP = *Aristida purpurea*, SI = *Sporobolus airoides*, BJ = *Bebbia juncea*, EF = *Encelia farinosa*, HA = *Hymenoclea salsola*, AD = *Ambrosia dumosa*, EA = *Eriogonum fasciculatum*, LT = *Larrea tridentata*, and NO = none (control, no native vegetation).

Summary of the performance of native perennial species with *Bromus rubens* in our greenhouse competition experiment and correlational field study, compared with Brooks (2009), who conducted a similar correlational study in the Mojave Desert. Species were ranked as poor, medium, or good in their ability for reducing *Bromus* biomass (greenhouse competition experiment) and for supporting low amounts of *Bromus* in the field (i.e. a 'good' rating indicates that *Bromus* is sparse below a species' canopy).

Species	This study: competition	This study: field	Brooks (2009): field
Ambrosia dumosa	Medium	Medium	Good
Bebbia juncea	Good	Good	Good
Coleogyne ramosissima	—	Medium	Medium
Eriogonum fasciculatum	Good	Medium	Medium
Hymenoclea salsola	Medium	Poor	Medium
Krameria erecta	—	Poor	Medium
Larrea tridentata	Medium	Poor	Medium
Psorothamnus fremontii	—	Medium	Poor
Salazaria mexicana	Good	Good	Poor
Thamnosma montana	—	Good	Poor

VI. Relationship to Other Recent Findings and Ongoing Work on This Topic

Interpretational summary for community and species invasion resistance experiments

The results of our community invasibility study provided variable support for our study hypotheses. The hypothesis that *Bromus* would better invade than *Schismus* within native vegetation was supported, but *Bromus* also became more firmly established in open plots without native vegetation than *Schismus*. Further factorial experiments including water availability, perennial plant neighbors, and elevation gradients may be useful for explaining performance differences in this study and previous correlation-based field studies. In the eastern Mojave Desert, for example, Brooks (1999) reported that *Bromus* had higher biomass below *Larrea tridentata* than in interspaces in wet and dry years. In contrast, *Schismus* shifted from higher biomass in interspaces in the dry year to higher biomass below *Larrea* in the wet year, suggesting a three-way interaction of invader identity, microsite, and precipitation. These relationships also can change along elevation gradients, as *Bromus* is constrained to below-shrub microsites at lower (drier) compared to higher elevations (Brooks and Matchett 2006).

The hypothesis that later successional communities and species would most strongly reduce invader success was mostly rejected. However, results did depend on the particular native community and species. The early forb community significantly decreased exotic biomass in both N treatments, the only community to do so, and was less invaded than later successional communities. Conversely, the early grass community performed poorly, and the early shrub community was similar to the late shrub community. Species within community types displayed variation in the species monoculture plots, suggesting potential for combining species by growth forms in different ways for maximizing community resistance to invasion. For example, grouping the best-performing species from each community (e.g., *Sphaeralcea ambigua* from the early forb, *Sporobolus airoides* early grass, and *Encelia farinosa* early shrub) at a given level of species richness would appear to most effectively decrease community invasibility. On the other hand, the greater variety of resident growth forms could promote invasibility by creating more microsites and niches for invaders (Levine et al. 2004).

Traits of native species that would result in being most strongly competitive with the exotic C_3 (cool season) grasses remain uncertain. In moist years supporting annual plants, the exotic grasses germinate in fall/winter and vigorously grow and produce seed in March-April when temperatures warm (Beatley 1974). Species that have periods of active growth most closely corresponding are generally considered to have the greatest potential for competition between them (Booth et al. 2003). However, simple correspondence of native and exotic C_3 species does not exist in the Mojave Desert, where an offset of only a month in the timing of active growth between native species within a photosynthetic pathway can affect competitive relationships with exotic grasses (James et al. 2006). Vigorous growth periods of the native species used in our experiments do overlap with those of the exotic grasses in spring (March-April; Beatley 1974), but as Corbin and D'Antonio (2004) noted, occupancy of space or other interference can affect species relationships even if growth periods of the species do not overlap. We did not find a strong relationship of native plant cover with exotic biomass, consistent with a non-manipulative field study in the eastern Mojave Desert that reported no relationship between native plant size and the cover of *Bromus* (Abella et al. 2011). While plant size often determines competitive ability in more mesic ecosystems, other traits such as canopy architecture, timing of germination, and soil modification related to fertile islands (resulting in facilitation rather than competition) may be more important in deserts. Interestingly, the species that best reduced invasion were those (e.g., *Sphaeralcea ambigua* and *Encelia farinosa*) that do not develop well-established fertile islands (Abella 2010).

Our third hypothesis, that N addition increases habitat invasibility, was supported, while our fourth, that communities reducing soil nutrients to the lowest levels would be least invasible, was not. Nitrogen addition in the control and early grass communities boosted exotic grass biomass production to be near or exceed a 100 g/m^2 threshold estimated for fire spread in the Mojave Desert (Rao et al. 2010). However, although N addition promoted exotic biomass in all native communities, invasibility of the early forb community was the least affected by N addition (Fig. 1). Given that our amount of N addition (3.4 g/m^2/yr for each growing year) exceeds current rates of N deposition (e.g., 0.3-0.8 [Rao et al. 2010] and 3.2 g/m^2/yr [Brooks 2003]) reported in the Mojave Desert, this community may reduce invasibility even if anthropogenic N deposition increases. Despite the fact that the early forb community was the most resistant to invasion when N was added compared to other communities, this community did not reduce soil N or P to its lowest levels as we had hypothesized. Manipulating other resources, such as water, would be useful in future invasibility experiments to evaluate if competition for resources other than soil nutrients or if other factors (e.g., allelopathy) impacted invasion resistance.

One of our main findings was that some native communities and species monocultures reduced the biomass of exotic annual grasses relative to controls (no native vegetation) to levels far below the Mojave Desert 'fire threshold' (Rao et al. 2010). This finding is unique, as nearly all previous research with exotic annual grasses in southwestern arid lands has focused on the one-way interactions of the effects of the exotics on natives (and not the effects of natives on the grasses) or have found that native species facilitate the establishment of the exotics (e.g., Brooks 1999, DeFalco et al. 2003). Our results have important implications for post-fire restoration efforts in the Mojave Desert. Because the biomass of native plants can facilitate fire spread when interspaces have filled with exotic annuals, experimenting with different densities of natives than used here is an important research need. Knowledge of the optimum density, biomass, and community composition of natives needed to reduce exotic species biomass to well below burn thresholds would be useful from fire management and restoration perspectives since establishing native plants is difficult and costly in arid lands.

Interpretational summary for the greenhouse competition and correlational field study

Brooks (2009) is the only other study known to us that has compared relationships in the native species versus *Bromus* direction (as opposed to *Bromus* effects on natives) among an array of species in southwestern deserts. Brooks (2009) compared *Bromus* biomass below 29 native perennial species in the southwestern Mojave Desert. While not all species were the same between Brooks (2009) and our study, the large numbers of species included in the studies enabled a relative ranking of species relationships with *Bromus*. We were able to compare 10 species in Brooks (2009) that were included in our field study, six of which also were included in our greenhouse experiment. Within the studies, we ranked these 10 species relative to all species included in a respective study (27 in our greenhouse experiment, 16 in our field study, and 29 in Brooks [2009]) into lower, middle, and upper thirds in their performance versus *Bromus*.

Eight of the 10 species were within one performance category among studies, while two species differed substantially. For example, *Bebbia juncea* consistently ranked as 'good' for both reducing *Bromus* in the greenhouse and supporting low amounts of *Bromus* cover in our and the Brooks (2009) field studies. *Eriogonum fasciculatum* ranked as 'good' in the greenhouse and 'medium' in the two field studies, and *Ambrosia dumosa* consistently ranked as 'medium'. Species that ranked 'poor' in our field study, such as *Krameria erecta*, ranked no better in Brooks (2009) than 'medium'. *Salazaria mexicana* and *Thamnosma montana* were the most disparate species, ranking 'good' in our study, but 'poor' in Brooks (2009).

Variability was high in performance among individuals within a species in both our studies and Brooks (2009), where standard errors of the means were as large or nearly as large as means for several species. Brooks (2009) highlighted two major spatial scales of variability in native species relationships with *Bromus*: broad landscape scales such as elevation gradients, where *Bromus* is typically most abundant at middle elevations, and within-site variation where microsites such as interspaces and canopies of perennial plants are important. He further noted that *Bromus*-native species relationships can shift with elevation. For example, *Bromus* may be closely associated with *Larrea tridentata* at lower elevations, but as abundant or more abundant in interspaces or below perennials other than *Larrea* at cooler and moister higher elevations. Further evaluating the potential interactions of landscape gradients (e.g., elevation) with perennial plants in affecting the distribution of *Bromus* could be useful future research.

While we did not find that the traits of biomass production in the greenhouse experiment or plant size in the field study were correlated with native species performance versus *Bromus*, other traits could be important. Some of the many traits of potential importance for perennials could include: seasonality of growth, canopy morphology, life span, degree and nature of fertile island formation, successional affiliation, literfall and decomposition, allelopathy, and rooting habit/mycorrhizal associations. For example, in a Mojave Desert field experiment, James et al. (2006) reported that the seasonality of growth of the native shadscale saltbush (*Atriplex confertifolia*) more closely corresponded with that of the exotic annual Arabian schismus (*Schismus arabicus*) and was a better competitor with *Schismus* than the perennial Parry's saltbush (*Atriplex parryi*). De Soyza et al. (1997) found that differences in canopy morphology among *Larrea tridentata* individuals influenced microclimates and associated native annual communities. This observation suggests that differences in canopy morphology both within and among species could influence the growing environment for *Bromus*. Based on observing distributions of native annuals in the Mojave Desert, Muller (1953) suggested that perennials with shorter life spans harbored fewer annuals. This supposition appears consistent with our field data for some species but not others. For instance, *Bebbia juncea* supported little *Bromus* cover and was classified by Bowers et al. (1997) as a short-lived perennial with an estimated maximum life span of 20 years. However, *Eriogonum fasciculatum* and broom snakeweed (*Gutierrezia sarothrae*) Britton and Rusby) also are considered short lived with estimated life spans of 20 years, but these species harbored intermediate amounts of *Bromus*. In addition to other traits, life span could influence the degree and nature of fertile island formation (Holmgren et al. 1997). Thompson et al. (2005) showed that soil properties such as nitrogen mineralization differed below canopies of three late-successional shrub species in the northern Mojave Desert. It could be hypothesized that species with shorter life spans, often with early successional affiliations (Bowers et al. 1997), do not form well-developed fertile islands and hence would be less favorable for *Bromus* growth. The five species that harbored the least amount of *Bromus* in our field study all are considered as early successional based on Abella's (2010) successional classification of Mojave Desert species. With the exception of *Hymenoclea salsola*, species that supported the greatest cover of *Bromus*, such as *Krameria erecta* and *L. tridentata*, are classified as late successional.

Litterfall, allelopathy, and rooting habit/mycorrhizal associations could further influence the growing environment for *Bromus* near perennial plants. Strojan et al. (1979) reported that yearly litterfall amounts in grams per shrub varied by an order of magnitude among six shrub species in the northern Mojave Desert. Depending on decomposition rates, this variation in litterfall could result in different thicknesses of litter layers below shrubs, which could positively or negatively or not influence *Bromus* establishment. Gray and Bonner (1948) isolated an allelopathic growth inhibitor in the foliage of *Encelia farinosa*, which was observed to harbor few annual plants. However, Muller (1953) subsequently found that an even stronger growth inhibitor was present in *Ambrosia dumosa*, a species that harbored abundant annuals. The significance of allelopathy as a factor influencing annuals below perennials remains unclear. The possible role of rooting habit also is unclear. Wallace et al. (1980) reported that *Krameria erecta* had more than twice the proportion of fine roots (of its total root system) in the upper 10 cm of soil among nine perennial species in the northern Mojave Desert. It could be hypothesized that this shallow rooting intensifies competition against shallow-rooted annuals, yet *K. erecta* harbored the greatest cover of *Bromus* in our field study. Since *K. erecta* also can be a root parasite on other perennial plants (Griffith 1991), which could influence nutrient contents in soils below its canopy, these observations suggest that exploring the possible influence of rooting ecology in *Bromus*-native species relationships may be a useful topic for future research. Similarly, Titus et al. (2002) reported that *Baileya multiradiata* had the greatest concentration of arbuscular mycorrhizae among 15 Mojave species. *Baileya multiradiata* was one of the species that facilitated *Bromus* growth in the greenhouse experiment, and it is unclear if mycorrhizal associations influence interactions with *Bromus*.

While traits such as fertile island formation may be less important in native annual species interactions with *Bromus*, other traits such as seasonality of growth, water requirements, and resource use discussed above for perennials may also be important for annuals (e.g., DeFalco et al. 2003). In addition, the potential interaction of perennial plants with associated native annual communities in influencing relationships with *Bromus* should be examined. For example, the most competitive native vegetation with *Bromus* could be a competitive perennial species paired with native annuals most competitive with *Bromus*, if such native vegetation types exist.

Since early work in the 1940s and 1950s (Went 1942, Muller 1953, Muller and Muller 1956) and with few exceptions such as Brooks (2009), little research has been directed at among-species differences in associations with annual species in southwestern deserts. This early work also concentrated on associations with native annuals, with less emphasis on exotics like *Bromus*. Much contemporary work has further focused on the effects of exotic annuals on native species, rather than which native species most strongly influence exotics. As a result, little research is available to help identify which native species could be amenable to control strategies for *Bromus* and whether competition from native species is a feasible treatment for reducing exotic plants.

For competition by native plant species to be an effective treatment for controlling exotics, the native species must: (1) compete with and reduce the exotic, (2) become reliably established via seeding or planting on sites where the exotic grows, and (3) be amenable to propagation and plant material development so that sufficient quantities of the species is available for treatments at operational scales. Native species treatments have shown mixed success at reducing exotic plants, either in the context of oversowing the native into an existing stand of the exotic, or following treatment of the exotic by herbicide or other methods. For example, Bakker and Wilson (2004) found that seeding a mixture of native species reduced the number of plots invaded by the exotic perennial grass crested wheatgrass (*Agropyron cristatum*) by 33% in Saskatchewan grasslands. Similarly, oversowing the native annual forb firewheel (*Gaillardia pulchella*) into existing stands of the exotic annual forb bastardcabbage (*Rapistrum rugosum*) All.) reduced productivity of the exotic by up to 72% along Texas roadsides (Simmons 2005). However, neither Thacker et al. (2009) nor Stevens and Fehmi (2009) found that seeding native perennial grasses reduced exotic grasses (including *Bromus tectorum* and buffelgrass [*Pennisetum ciliare*) of southwestern arid lands. In contrast, Seabloom et al. (2003) found that seeding native perennial grasses into California exotic annual grasslands (including *Bromus*) reduced seed production and biomass of the exotics.

VII. Future Work Needed

We suggest the following topics as those among the most important for advancing burn revegetation in southwestern arid lands:

- Early successional native perennials as a group displayed great potential for competing with exotic annual grasses. However, not all early perennials performed well, and we only tested a small proportion of the total number of possible species. We suggest that future research target the early perennial forb and shrub group for screening additional species for their competitive ability and amenability to revegetation.

- Once competitive native species are identified, much more work needs to be done to increase the establishment rates of these species through revegetation treatments on burn areas. Because our review of natural post-fire recovery patterns indicated that many of the competitive native perennials are the early colonizers of burns, we know that these species do have the abilities to colonize post-burn environments. Techniques to augment these post-fire establishment rates would be useful. Techniques such as protecting seedlings, developing more effective seeding treatments (e.g., by optimally timing seeding), and establishing revegetated islands to promote seed dispersal warrant further research.

- Determining minimum densities of competitive natives that must be established to reduce exotic biomass below typical Mojave Desert fire thresholds would help managers plan how intensive their revegetation treatments must be.

- Processes of post-burn succession are especially slow in deserts. A long-term perspective would be useful to evaluate dynamics in the revegetation communities themselves. For example, for late-successional species, it is unclear at what plant age the interactions of natives with the exotic grasses might change from competitive (of native vs. exotic) to facilitative. This dynamic likely hinges on the rates of fertile island formation, which are poorly understood. Firmly established fertile islands generally promote exotic species biomass. It will be challenging to identify ways to incorporate late-successional native species (that do form fertile islands) into revegetation plans, as maintaining early successional native communities for many decades may not be desirable if the area burned (and hence the area of early successional communities) continues to rise.

- Results were encouraging for identifying native species that can both compete with exotic grasses and be amenable to revegetation treatments on burns. *Sphaeralcea ambigua* (globemallow) was the most competitive native species with exotic grasses, and it also performed well (≥ 50% survival) in outplanting trials. Unfortunately, seeding was not successful. Developing methods (including optimal timing) to make seeding more effective is a critical research need. This research has identified multiple native species (from a pool of 12; more should be tested) that can reduce exotic annual grasses, and so a next challenge is to improve methods to establish these species.

VIII. Deliverables Cross Walk

Proposed	**Delivered**	**Status**
2 Masters Theses	With approval from JFSP, this project was switched from graduate students to research staff supported by undergraduate students. Hence, the theses were converted to publications.	Not applicable
One or More Refereed Publications	Three articles are published or in press. An additional two articles are in review.	Completed
One or More Technical Publications	Five articles were published in Mojave Applied Ecology Notes, the applied research newsletter targeted towards resource managers in the Mojave Desert	Completed
Two Conference Presentations	14 conference presentations and invited talks delivered	Completed
Two Field Demonstrations/Tours	Land managers participated directly in the project set up field work and maintenance. A final tour reflecting year 3 findings on the burn revegetation portion, which we will complete in spring 2011, is planned.	In progress
Research Dataset	Provided to the National Park Service	Completed
Web site	http://www.unlv.edu/staff/cengel/JFS.htm	Completed, to be updated with ongoing results
Final JFSP Report	Final report for 07-1-3-24	Completed

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X. Additional Reporting (Appendices and other inputs to JFSP)

A. We have uploaded two published manuscripts (below) and an in press manuscript as three separate files.

B. We have uploaded five non-peer reviewed technical articles (combined into a single file) providing summaries of management implications of the ongoing project.

C. We have uploaded all posters (combined into a single file) presented at conferences.

Final Report

Abella, S.R., D.J., Craig, S.D. Smith, and A.C. Newton. 2010. Revegetating burned arid lands: identifying successful native species using trait and competition analysis. Final Project Report (JFSP Project Number: 07-1-3-24). December 31, 2010, Las Vegas, NV.

Website

Project home page, fully outlining the project and will be updated with ongoing results: http://www.unlv.edu/staff/cengel/JFS.htm

Professional Presentations and Invited Talks

Abella, S.R. Fire and climate change in American Southwest arid lands. Guest lecture for GS-0401 fire management specialist education program, University of Nevada Las Vegas, Las Vegas, NV. 8 December 2009.

Abella, S.R., and D.C. Craig. Identifying candidate native species for revegetating desert wildfires. Poster presentation at the 4th International Fire Ecology and Management Congress: Fire as a Global Process, Savannah, GA. 1 December 2009.

Suazo, A.A., D.J. Craig, and S.R. Abella. Seed removal by granivorous ants and rodents in burned and unburned Mojave Desert habitats. Poster presentation at the 94th annual meeting of the Ecological Society of America, Albuquerque, NM. 6 August 2009.

Abella, S.R., E.C. Engel, D.J. Craig, and A.A. Suazo. Post-fire plant recovery and restoration: a systematic review and Clark County chronosequence. Oral presentation (invited) at the 10th annual meeting of the Eastern Nevada Landscape Coalition, Fire rehab in the 21st century: the Southern Nevada Complex, anomaly or the new status quo? Ely, NV. 13 June 2009.

Abella, S.R., E.C. Engel, D.J. Craig, and A.A. Suazo. Update on completed and ongoing fire projects by UNLV. Oral presentation (invited) to resource managers of the Mojave Desert Initiative, Interagency Office, Las Vegas, NV. 7 May 2009.

Abella, S.R. Fire and climate change in American Southwest arid lands. Oral presentation (invited) at the Environmental Biology Seminar Series, University of Nevada Las Vegas, Las Vegas, NV. 23 April 2009.

Craig, D.J., J.E. Craig, and S.R. Abella. Road corridor surveys alone may not reliably detect extent of exotic annual plant distributions. Poster presentation at the 2009 George Wright Society Biennial Conference on Parks, Protected Areas, and Cultural Sites, Portland, OR. 3 March 2009.

Abella, S.R., E.C. Engel, D.J. Craig, S.D. Smith, C.L. Lund, A.C. Newton, and J.L. Gunn. Post-fire plant recovery and restoration in the Mojave and Sonoran Deserts of western North America. Oral presentation (invited) at the Desert Tortoise Council symposium, Mesquite, NV. 21 February 2009.

Abella, S.R. Post-fire plant recovery in the Mojave and Sonoran Deserts of western North America. Poster presentation at the Wildfires and Invasive Plants in American Deserts conference, Reno, NV. 9 December 2008.

Craig, D.J., J.E. Craig, and S.R. Abella. Implications for management prioritization of exotic annual weed monitoring near roadsides in the eastern Mojave Desert, USA. Poster presentation at the Wildfires and Invasive Plants in American Deserts conference, Reno, NV. 9 December 2008.

Suazo, A.A., D.J. Craig, and S.R. Abella. Seed removal by granivores in burned Mojave Desert habitat: implications for revegetation. Poster presentation at the Wildfires and Invasive Plants in American Deserts conference, Reno, NV. 9 December 2008.

Abella, S.R., and M.N. Rees. Vegetation monitoring and analysis at Lake Mead National Recreation Area. Oral presentation at the Great Basin Cooperative Ecosystem Studies Unit annual meeting, Reno, NV. 8 December 2008.

Craig, D.J., J.E. Craig, and S.R. Abella. Exotic annual plant invasions and their relationships to roads and native perennial species in the Mojave Desert, southwestern USA. Poster presentation at the 35th Natural Areas Association conference, Nashville, TN. 15 October 2008.

Abella, S.R., and E.C. Engel. A regional chronosequence of fire succession and network of long-term monitoring plots. Oral presentation (invited) to resource managers of the Mojave Desert Initiative, Interagency Office, Las Vegas, NV. 26 March 2008.

Technical/Non-Peer Reviewed Publications

Abella, S. 2009. Synthesis completed of post-fire recovery of native perennials in the Mojave, Sonoran Deserts. Mojave Applied Ecology Notes 2(2):5.

Craig, D. 2009. Joint Fire Science update. Mojave Applied Ecology Notes 2(1):5-6.

Craig, J. 2008. The Desert and Dryland Forest Research Group presents eight posters: Wildfires and Invasive Plants in American Deserts. Mojave Applied Ecology Notes 1(4):4-6.

Craig, D. 2008. Joint Fire Science grant update. Mojave Applied Ecology Notes 1(2):4.

Craig, D. 2008. Joint Fire Science grant update. Mojave Applied Ecology Notes 1(1):4.

Peer-Reviewed Publications in Print/in Press

Abella, S.R., D.J. Craig, L.P. Chiquoine, K.A. Prengaman, S.M. Schmid, and T.M. Embrey. 2011. Relationships of native desert plants with red brome (*Bromus rubens*): towards identifying invasion-reducing species. Invasive Plant Science and Management (in press).

Craig, D.J., J.E. Craig, S.R. Abella, and C.H. Vanier. 2010. Factors affecting exotic annual plant cover and richness along roadsides in the eastern Mojave Desert, USA. Journal of Arid Environments 74:702-707.

Abella, S.R. 2009. Post-fire plant recovery in the Mojave and Sonoran Deserts of western North America. Journal of Arid Environments 73:699-707.

Publications under Review

Suazo, A.A., D.J. Craig, and S.R. Abella. Seed removal patterns in burned and unburned Mojave Desert habitats: implications for restoration. Restoration Ecology.

Abella, S.R., D.J. Craig, S.D. Smith, and A.C. Newton. Factors influencing the establishment of exotic grasses in the Mojave Desert and potential for reducing plant community invasibility. Ecological Applications.

Additional Products in Preparation

We anticipate writing up a manuscript on the burn planting/seeding results once the year 3 results are completed (anticipated spring 2011). We only committed to collecting two years of data, which are reported here, but we would like a third year of data for a manuscript. We also are in the process of submitting a manuscript for review on the supplemental seed removal study as part of the seeding component.