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## Exploring the Seed Bank Dynamics of Red Brome: Longevity, Density, and Relationship to Fire

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EXPLORING THE SEED BANK DYNAMICS OF RED BROME:  
LONGEVITY, DENSITY, AND RELATIONSHIP TO FIRE

By

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Bachelor of Fine Arts  
University of Tennessee, Knoxville  
2002

A thesis submitted in partial fulfillment of  
the requirements for the

Master of Science in Environmental Science

Department of Environmental Studies  
School of Environmental and Public Affairs  
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The Graduate College

University of Nevada, Las Vegas  
May 2012

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## THE GRADUATE COLLEGE

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**Benjamin S. Jurand**

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**May 2012**

## ABSTRACT

### **Exploring the Seed Bank Dynamics of Red Brome: Longevity, Density, and Relationship to Fire**

By

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This research explores several untested aspects of the seed bank characteristics of red brome (*Bromus rubens*), an invasive annual grass in southwestern United States arid lands. Red brome is a formidable competitor to native plant species, both annual and perennial alike, and produces many seeds that germinate easily. The stalks of red brome contribute continuous-cover fuel loads that facilitate wildfires destructive to mature native Mojave Desert plant communities. This makes it a priority species for land managers, particularly when dealing with recovery after fire.

This project addressed questions related to the longevity of red brome seeds in soil seed banks and the dynamics of seed densities after wildfires. After being experimentally buried, proportions of viable seeds in the soil were substantially reduced over time. Only six percent of seeds remained viable after one year of burial and 2.6 percent of seeds remained viable after two years of burial. Greater proportions of seeds lost their viability at greater burial depths. Soil seed bank density patterns of red brome were spatially variable across a 31-year time-since-fire chronosequence, and generally were not related to time-since-fire. However, some fires showed significant differences between microsites in burned and unburned areas. While fire disturbances did not

necessarily promote greater seed densities of red brome over time in all burned areas, the youngest fire sites sampled in this study (six years after burning) exhibited little difference between burned and unburned areas. This study confirmed that, when red brome is a major component of above-ground vegetation, the species dominates the desert soil seed bank. Future research should consider longevity of seeds beyond two years, as well as comparing above-ground growth of red brome with seed densities observed in the greenhouse emergence study.

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# CHAPTER 1

## INTRODUCTION

### Purpose of This Study

Invasive plant species pose serious threats to the ecosystems they invade. Not only do they compete with native plant species for resources and space but can also alter the structure and functioning of native ecosystems by changing such characteristics as nutrient cycling and disturbance regimes (D'Antonio & Vitousek, 1992). Understanding the mechanisms that influence the spread of an invasive species and the impacts those species have on native environments is key to developing management strategies. For example, identifying characteristics of invasive species and invaded habitats can aid efforts to prevent future invasive species introductions. Invasive species are particularly problematic in the arid southwestern United States, where the presence of several exotic grass species has been tied to the increasing frequency and severity of widespread wildfires. Red brome (*Bromus rubens*) is an important exotic species in the Mojave Desert and is noted by managers for its potential to outcompete native species and promote wildfires (Brooks, 2009).

Management strategies to address annual species like red brome often rely on reducing the number of seeds in a population. While much has been studied regarding *B. rubens* and its ecological relationships to other species and to the landscape, there are some notable gaps in our knowledge, particularly related to seed dynamics. This project addressed questions related to the longevity of red brome seeds and the dynamics of seed densities as impacted by fire disturbances. The two studies that comprise this research explore different aspects of the seed bank characteristics of *B. rubens*: (1) how long seeds remain viable (i.e., dormant) in the soil, and in what proportions, and (2) what are the effects of fire over time on the density of red brome

seeds in the soil. To empirically test the effects of burial duration and depth, seeds were placed in enclosures and buried in the field. After four burial duration treatments, enclosures were recovered and viability (or nonviability) of each seed was assessed. To test for effects of burning on the seed bank density and composition over time for both natives and *B. rubens*, soil seed banks were also sampled from burned and unburned areas of fires that occurred between six and 31 years ago.

## Research Questions

### Study 1: Seed Longevity

The purpose of this study was to empirically examine the longevity of *B. rubens* seeds in the soil. Seed enclosures were buried in the field to test the effects of burial duration and burial depth on seeds from recent Mojave Desert fire sites. The following research questions (and predictions) drove the design and analysis of the study:

(1) How long do seeds remain viable in the seed bank?

We anticipated that over time the proportion of viable (i.e., dormant) seeds would decrease. Specifically, we expected that after one year, roughly two percent of seeds would remain viable, following Wu and Jain's (1979) estimation. We expected further reduction after two years, following Brooks (2002).

(2) Are seed germination rates affected by burial depth?

Since burial depth has been shown to decrease viability in similar brome species (Narwal *et al.*, 2008; Jensen, 2009), we expected proportions of viable *B. rubens* seeds to decrease with greater burial depth.

(3) Do seeds from burned areas exhibit different viability patterns than seeds from unburned areas?

Fires cause numerous changes that impact seed banks, including notable differences between burned and unburned areas in soil chemistry, addition of

nutrients, soil sterilization of microbes, and the removal of above-ground vegetation (Keeley & Fotheringham, 2000). However, it is unknown whether any of these factors play a role in the growth, development, and/or viability of red brome seeds. While plant growth and development can be affected by changing soil and environmental properties, less is known about the effects on seed viability. We expected little to no effect on the proportion of viable seeds in areas burned by wildfire versus those left unburned.

### Study 2: Seed Bank Density and Composition

Exploring the dynamics of seed bank density and composition change in burned areas following fire can help us understand the functional ecology of red brome seeds in relation to other species as well as to fire disturbances. It can also inform management strategies that address seed production and dispersal in areas disturbed by fire. When red brome re-colonizes a burned area, it may outcompete native species by interfering with native species reestablishment. This study sought to bridge gaps in our understanding of the seed bank characteristics of red brome; particularly, whether the presence of a wildfire affects the density of *B. rubens* in space and over time, and how this density compares to other species. We sampled soil seed banks at the sites of 12 fires that burned within the last 30 years to address the following research questions:

- (1) How do *B. rubens* seed bank densities change as a result of fire? How do these densities change over time?

Supporting Brooks' (2002) observation that over time red brome densities in burned areas quickly return to or exceed pre-burn levels, we expected equal or greater seed densities of *B. rubens* in burned than in unburned areas, particularly at older fire sites. We anticipated that the ratio of *B. rubens* to native seeds would change as a function of time-since-fire. Since *B. rubens* cover is reduced following fires, it is likely that in the early years after a fire, *B. rubens* seeds are

reduced along with native species seeds (Abella *et al.*, 2009). As time-since-fire increases, we anticipated *B. rubens* seeds to be greater in burned areas overall.

(2) How do spatial variations in seed bank densities between microsites differ between burned and unburned areas?

Since *B. rubens* tends to be densest under shrub canopies, we expected this pattern to be variable over time, with greater relative densities in interspaces in the youngest fires (following Abella *et al.*, 2009), but over time we expected less difference between microsites in burned areas as densities are restored under shrubs. Greater densities in interspaces than under shrubs would indicate a change from the normal patterns and support the grass-fire theory that burned areas favor grasses.

(3) How are native species seed bank densities affected by fire? Is there a relationship between seed densities of *B. rubens* and native species?

If *B. rubens* seed densities were greater in burned areas, we expected native densities to be lower in burned areas, particularly in the oldest fires.

(4) How is the composition of the seed bank affected by fire?

Species composition is variable in the environment, even in the same shrub community (Engel & Abella, 2011). We did not expect a pattern in species composition between fires, but expected more *B. rubens* and less natives in burned areas.

## CHAPTER 2

### LITERATURE REVIEW

#### Introduction

To gain a better understanding of *Bromus rubens* and its ecological relationships, I conducted a literature review on the ecology of red brome and its impacts in the Mojave. I also examined articles on the ecology of seed banks. I searched article databases Google Scholar and Academic Search Premier with keywords “*Bromus rubens*,” “red brome,” “seed banks,” “Mojave Desert,” “*Bromus tectorum*” and “grass-fire cycle,” as well as article reference lists for relevant publications.

*B. rubens*, also known as red brome, foxtail brome, and foxtail chess, is a winter annual grass native to the Mediterranean areas of Southern Europe, Northern Africa, as well as Southwestern Asia (Brooks, 2000). It is invasive to the Mojave Desert, where it has become abundant in both disturbed and undisturbed areas. Red brome, like other exotic winter annual grasses, degrades invaded ecosystems by adversely affecting their structure and function (Reid *et al.*, 2006). Populations of *B. rubens* pose serious threats to native plant species—annual and perennial alike—by reducing native species richness and diversity (Salo, 2004). The species also creates fine fuels for wildfires that substantially alter or transform native ecosystems ill-adapted to widespread or frequent fires (Brooks, 2000). The increased spatial continuity of fine fuels under native perennial species’ canopies threatens to convert shrubland to grassland ecosystems, a result of increased frequency, extent, and intensity of fires (Salo, 2004). Wildfires have the potential to inflict both economic and ecological damage, and negatively affect the recreational and aesthetic qualities of the natural landscape.

As with many other modern plant invasions, the introduction of *B. rubens* to the Southwestern U.S. is attributed to human activities. Herbarium records indicate that *B.*

*rubens* was brought to North America sometime before the 1880s and moved west with human migration (Salo, 2005). It accompanied immigrants and their cargo during the Gold Rush and subsequent development of California, and was likely present in agricultural imports and livestock feed (Salo, 2005). Red brome became common in the Las Vegas area and the greater Mojave region circa 1920. It proliferated rapidly throughout the Southwestern U.S. to become fully established by the 1950s (Salo, 2005). More recently, Brooks (2009) reported that the Mojave Desert has seen a marked increase in non-native winter annual species cover from 9 percent in 1970 to 13 percent by the end of the 1990s. Increasing disturbances from the built environment including roadway construction, highway and off-road vehicle traffic, and altered hydrology (i.e., water run-off), as well as the changes in fire regimes contribute to the continued dispersal of seeds and the spread of red brome today (Reid *et al.*, 2006).

By using resources and occupying spaces otherwise available to native annuals, red brome has the potential to outcompete and exclude native annual species. *B. rubens* can germinate with as little as 2.5 cm of rainfall, considerably less than native annual species (Beatley, 1966). Indeed, in years of high rainfall, early establishment and prolonged growth of *B. rubens* leads to greater soil moisture and nutrient uptake, outcompeting native annuals in the process (D'Antonio & Vitousek, 1992).

*B. rubens* is most successful in more mesic microhabitats such as beneath shrub canopies of native perennial species and along ephemeral washes (D'Antonio & Vitousek, 1992). Although it has been observed between sea level and 1,300 m, *B. rubens* is most abundant at elevations above 800 m in the Mojave Desert (Brooks, 2000). In addition to being identified in traditionally invaded disturbed areas, it can also become established in relatively undisturbed areas making it an important species to land managers (Brooks, 2009).



Red brome usually germinates in the fall, when temperatures are cooler and conditions are moister, particularly following heavy rains (Brooks, 2000). Depending on precipitation, seeds can also germinate through the winter and spring. Winter temperatures that remain above freezing, as well as adequate soil moisture during the spring growing season, are both vital for the survival of *B. rubens* seedlings and the completion of its reproductive cycles (Hulbert, 1955; Brooks, 2009).

Seedling growth proceeds slowly in winter months and increases with rising spring temperatures. Peak vegetative and reproductive development, including flowering, occur in the spring when densities can reach as high as 6,000 plants/m<sup>2</sup> (Salo, 2004). Flowering continues into late spring when water stress kills the plants (Beatley, 1966). Once the plants die, their dried stalks often remain upright in the soil for one to three years, adding fine fuels for wildfires (Brooks, 2000).

Despite the fact that *B. rubens* requires relatively little water to germinate, less than 1 cm of rainfall in fact (Brooks, 2000), populations have been known to crash in years of severe drought. If soil moisture is too low during the growing season, plants will not reach reproductive maturity, allowing for the potential recovery and restored dominance of native annuals. To recover from population crashes, it is believed that *B. rubens* seeds must be dispersed from nearby populations or from favorable microsites, rather than persist in the soil seed bank (Salo, 2004).

### Viability and Longevity of Seeds

Red brome is a prolific seed producer. Individual plants can produce varying numbers of seeds, approximately 76 seeds in natural settings on average (Wu & Jain, 1979). Smith *et al.* (2000) reported greater numbers in their study in the Nevada Test Site, with individual *B. rubens* plants generating between 97 and 235 seeds (depending on microsite) at ambient CO<sub>2</sub> levels. When red brome seeds are shed, they are

dispersed via wind and usually land on the ground within 1 m of the mother plant, or may also be dispersed by small mammal species (Hulbert, 1955). Once on the ground, many seeds are trapped by litter or covered by soil. This upper layer of soil (0 to 5 cm) and the litter layer are the most productive part of the soil seed bank (Abella *et al.*, 2009).

The covering or burial of seeds in the soil can play a role in the long-term carryover of viable seeds. While the effects of burial on the longevity of viable *B. rubens* seeds remain unclear, research on similar species can suggest hypotheses as to how red brome seeds behave. For example, buried seeds of *B. tectorum* have been shown to exhibit less carryover than seeds that remain on the surface (Meyer *et al.*, 1997). Studies also suggest that buried seeds are more likely to germinate than seeds that remain uncovered, as Gleichsner and Appleby (1989) reported of *Bromus rigidus* seeds. The viability of *Bromus hordeaceus* and *Bromus sterilis* seeds has also been shown to decrease with increasing soil depth (Jensen, 2009). Additionally, as it relates to above-ground seedling growth, in a greenhouse experiment on *B. rubens* emergence after germination at different depths, Abella *et al.* (2011) found the greatest emergence occurred in surface-sown seeds and declined with increasing burial depth. This suggests that burial depth can affect not only seed viability, but seedling emergence as well.

While densities can vary spatially and temporally, red brome seeds, where present in the above-ground vegetation, often dominate seed banks. A study by Price and Joyner (1997) revealed that out of 33 species found in a seed bank, *B. rubens* was the sixth most abundant, producing numbers far greater than is common in desert soils. While it may not be surprising that red brome seeds can be abundant in seed banks, they are not likely to remain viable in the soil for long due to their high fecundity. *B. rubens* has been shown to exhibit between 70 and 100 percent germination (Wu & Jain, 1979; Corbineau *et al.*, 1992). This near-total germination rate indicates that most seeds from any given year are more likely to germinate and less likely to remain dormant from

season to season. In fact, in a census of dormant seeds in the soil, Wu and Jain (1979) noted as little as two percent of *B. rubens* seeds carryover from year to year. Brooks (2000) deduced that viable seeds only remain in the soil for two to three years, but did not test this directly. Most information regarding the longevity of *B. rubens* seeds in the soil is largely anecdotal, revealing a gap in our understanding of the population dynamics of red brome.

Red brome seeds exhibit different dormancy strategies than do the seeds of many native annual species (Salo, 2004). As an adaptation to variable resources, the seeds of many native annual species often delay germination or remain dormant in the soil beyond a single year, forming stable, age-structured seed banks of multiple generations (Rice & Dyer, 2001). In contrast, *B. rubens* and other *Bromus* species rely on the annual proliferation of seeds and do not maintain long-term seed banks (Salo, 2004). *Bromus tectorum* (cheatgrass), a similar and more comprehensively studied *Bromus* species, has been shown to produce seeds that are only conditionally dormant and have minimal carryover to subsequent seasons (Meyer et al., 1997).

Maintaining long-lived seeds is an especially useful adaptation to native annual plant species in the Mojave Desert, one that allows species to be sustained, even through unfavorable years (Venable et al., 1993). Venable and Brown (1988) describe dispersal and dormancy strategies as inversely correlated. Where *B. rubens* tends toward annual seed dispersal as its strategy, it is less likely that seeds remain dormant in the soil for an extended period of time. Still, even a small number of dormant viable seeds in the seed bank could help *B. rubens* regenerate after population crashes, emerging from the soil rather than being dispersed. This has implications after fire disturbances, as indicated by variable reduction of *B. rubens* abundance shortly following fire (Abella et al., 2009).

It has been noted that *B. rubens* seeds do exhibit some dormancy particularly during months of extreme temperatures and low precipitation (Corbineau et al., 1992). Young

seeds prefer to wait until the cooler, moister months of autumn and winter to germinate (Corbineau *et al.*, 1992). This suggests a similar high-temperature dormancy to that observed in *B. tectorum* seeds (Meyer *et al.*, 1997). Once conditions are suitable, most seeds will likely germinate, indicating a limit to the potential long-term dormancy (and therefore viability) of *B. rubens* seeds in the seed bank.

Smith *et al.* (2008) quantified the longevity of *B. tectorum* seeds and found that depending on precipitation levels, between 7.6 percent and 9.3 percent of seeds produced in a given year actually carried-over to the following year, with years of higher precipitation seeing less carryover than lower precipitation years. This suggests that low precipitation may facilitate *B. tectorum* seeds to enter a secondary dormancy, i.e., to reenter a dormant state following a period of non-dormancy and favorable conditions (Thompson, 2000). This allows for greater carryover of seeds to subsequent seasons (Meyer *et al.*, 1997).

#### Seed Bank Density and Composition

Dead stalks of red brome—that stay upright in the soil for up to three years (Brooks, 2000)—represent the bulk of the species' contribution of fine fuel for wildfires. While *B. rubens* tends to prefer more mesic microsites under shrub canopies (D'Antonio & Vitousek, 1992), it can also be found in open interspaces between shrubs. This provides additional connectivity between fertile shrub island communities, further enabling the spread of fire.

In this way, red brome has the potential to induce an ecosystem-changing process often referred to as the grass-fire cycle (D'Antonio & Vitousek, 1992). The process follows that the presence of fuel-providing species like *B. rubens* enables more widespread fires that threaten native plant communities. Once burned, mature shrub communities are destroyed leaving disturbed areas that can be quickly re-colonized by

invasive species. When reestablished, these invasive species further enable fires. Over time, these fires alter the plant community structures at the ecosystem level, favoring exotic grasses at the expense of native species (D'Antonio & Vitousek, 1992). Since many perennial plant species in the Mojave Desert are largely ill-adapted to widespread or frequent fire, charismatic, slow-growing, and long-lived native vegetation such as Joshua trees (*Yucca brevifolia*) and Mojave yuccas (*Yucca schidigera*) are often killed by fire and rarely resprout (Abella, 2010). These fire disturbances drastically alter native species composition, changing late-successional communities of long-lived perennial shrubs to perennial forbs (Abella *et al.*, 2009).

Red Rock Canyon National Conservation Area, a popular recreational area near Las Vegas, Nevada, has seen several of these widespread fires over the past few decades. More recently, in the 2005 and 2006 fire seasons, over 2,400 acres within the Red Rock Canyon Scenic Loop burned in wildfires. In the 2005 fire season alone, 2.5 percent of the total land area of the Mojave Desert burned (Brooks & Matchett, 2006), a considerable amount given that widespread fires have only begun to occur since the introduction and spread of exotic grasses like *B. rubens*. With the proliferation of red brome, fires such as these continue to pose a hazard to visitors and threaten to reduce or restrict resources, recreational uses, as well as aesthetic qualities.

Looking at related and often equally problematic brome species can bolster hypotheses about how *B. rubens* behaves in the environment. For example, it has been observed that *B. tectorum* can suppress growth of native species in the habitats it invades by growing rapidly in burned areas (D'Antonio & Vitousek, 1992). As time passes following burning, native seedlings can have increased difficulty competing with brome in disturbed areas, resulting in a reduction in native seed densities. In California mixed chaparral burns, Zammit and Zelder (1988) found altered seed bank compositions after fire. Seed densities of some species—particularly annuals—increased with more

time-since-fire. This suggests not only that fires can aid species regeneration by affecting seed banks densities after burning, but also that this effect can increase over time. It is unclear if this dynamic is exhibited in more arid desert ecosystems and with *B. rubens* in particular.

### Relationship to Fire

The effects of fire on native species communities and successional processes initiated by fire disturbances are not fully understood in arid environments (Engel & Abella, 2011). Exploring how fire influences seed bank structures of annual species like red brome can contribute to our overall understanding of the grass-fire cycle and successional processes initiated by fire. A fire disturbance initiates the natural process of secondary succession, where plant community structures evolve from early colonizing species to mature plant communities. High temperatures from fire can kill seeds in the soil, destroying both exotic and native seed banks in the process. This was supported in Abella *et al.* (2009), where red brome seedling emergence was observed to be reduced greatly when experimentally heated to 100°C. Additionally, in Abella *et al.* (2009), total cover (alive and dead) of *B. rubens* was reduced in burned areas as compared to unburned areas two years after the fire.

Despite such observations of diminished *B. rubens* populations in the early years following fire, Brooks (2002) notes that over time the abundance of red brome in burned areas often returns to or even exceeds pre-burn levels. This above-ground abundance may be reflected in the soil seed bank. It is generally assumed that most viable *B. rubens* seeds in the seed bank were shed in the previous growing season's seed production, with only a small portion of seeds carried-over from previous years (Wu & Jain, 1992). Additionally, as Hulbert (1955) estimates, a majority of seeds are dispersed

locally, most falling within 1 m of the mother plant. A greater density of plants in burned areas will likely be reflected in higher seed densities in the soil.

Less abundant red brome densities immediately after fire provide a small window of opportunity for managers to act in restoring burned areas. How quickly and easily red brome seed banks regenerate in burned areas may be influenced by the altered ecological structure of burned areas, as grass-fire theory would suggest. Fires cause numerous changes that impact seed banks, including notable differences between burned and unburned areas in soil chemistry, additions of nutrients, soil sterilization of microbes, and the removal of above-ground vegetation (Keeley & Fotheringham, 2000). Studies have also shown that plant growth can be stimulated following fire due to changing soil chemical properties and increasing nutrient availability, such as nitrogen (Raison, 1979). These increases can have lasting effects that linger for months to years (Blank *et al.*, 2003), possibly contributing to long-term changes in species composition following fire disturbances. When looking at cover of *B. rubens* two years after fire, Abella *et al.* (2009) found more live cover in burned areas than unburned areas, suggesting that favorable conditions in burned areas may enable greater *B. rubens* growth years after burning.

## CHAPTER 3

### METHODOLOGY

#### Overview

The two studies comprising this research, while both addressing different questions about the seeds and seed banks of *Bromus rubens*, employed much different methodologies. Study 1 (seed longevity) was an experimentally controlled treatment study that took place in the field. We empirically examined the longevity of *B. rubens* seeds under natural conditions by burying experimental seed banks *in situ* at varying depths in the field. Seed enclosures were recovered from the field after four burial duration treatments. Seeds were analyzed for viability in the laboratory. Variables included burial depth, burial duration, and burn status. Study 2 (seed bank density and relationship to fire) is an observational study employing a greenhouse method involving seedling emergence in a controlled environment. Soil seed bank samples were gathered from 12 historical fires in the vicinity of Red Rock Canyon National Conservation Area in Southern Nevada. Samples were placed in the greenhouse and seedlings allowed to emerge. Identified emerging species were then counted and analyzed.

#### Study 1: Seed Longevity

##### Study Area

Seven field plots were selected on areas of recent wildfire in the vicinity of Red Rock Canyon National Conservation Area outside of Las Vegas, Nevada (36°00'29N–36°08'35 N, 115°23'25 W–115°25'54 W). The fires took place between 2005 and 2007 and varied in size between 41 and 33,569 acres burned. All plots ranged in elevation from 1,030–1,273 m, where *B. rubens* is observed to be most abundant (Brooks, 2000). Seeds were gathered from each field site in May 2009, after mature plants flowered and



completed their reproductive cycles (Table 1). Each site's collection included plants from two fire conditions: areas burned in the recent fires and comparable adjacent areas that remained unburned. All seeds were placed in dry storage in the lab.

Table 1. Timeline of Study 1: Seed longevity

| May 2009                              | Sept. 2009             | March 2010         | Sept. 2010          | March 2011          | Sept./<br>Oct. 2011 |
|---------------------------------------|------------------------|--------------------|---------------------|---------------------|---------------------|
| Seeds gathered, placed in dry storage | Seed enclosures buried | 6-month collection | 12-month collection | 18-month collection | 24-month collection |

### Experiment Design

One hundred seeds were placed in each individual seed enclosure. Since most seed banks are densest between 0 cm and 5 cm depth (Abella *et al.*, 2009), we buried seed enclosures at 0, 2, and 5 cm. We also buried seed enclosures at 10 cm depth to represent an extreme boundary depth for seed burial. We used two types of seed enclosures for different depths. For buried seed enclosures at depths of 2 cm, 5cm, and 10 cm, the seeds were placed in sterile sand (all-purpose sand, supplied by Quikrete, Atlanta, GA) and nylon mesh bags. The mesh allowed for the transfer of moisture and soil microbes through the bags, but kept seed enclosures from being contaminated by seeds in the surrounding environment. For seed enclosures simulating surface seeds (or 0 cm burial depth), 100 seeds were placed atop sterile sand in pots. Fine mesh was glued to the top of each pot to prevent wind dispersal and introduction of outside seeds.

The seed enclosures were taken into the field and buried at the same subplot where the seeds were gathered. Burial of seed enclosures took place in September 2009, before *B. rubens* began germinating in the field (Table 1). Seed enclosures remained buried for durations of 6, 12, 18, and 24 months. At each field plot, the four burial duration treatments were randomly placed in 1 m × 1 m sub-plots. Seed enclosures were

placed in cylindrical wire mesh cages and buried in the soil at depths of 2 cm, 5 cm, and 10 cm (Figure 1). Seed enclosures for 0 cm treatments were placed in the wire cages so the surface of the sand was level with the surface of the soil. No additional soil was placed on the pots. After each time treatment elapsed, we returned to the field site to recover the seed enclosures for sifting and categorizing in the lab.

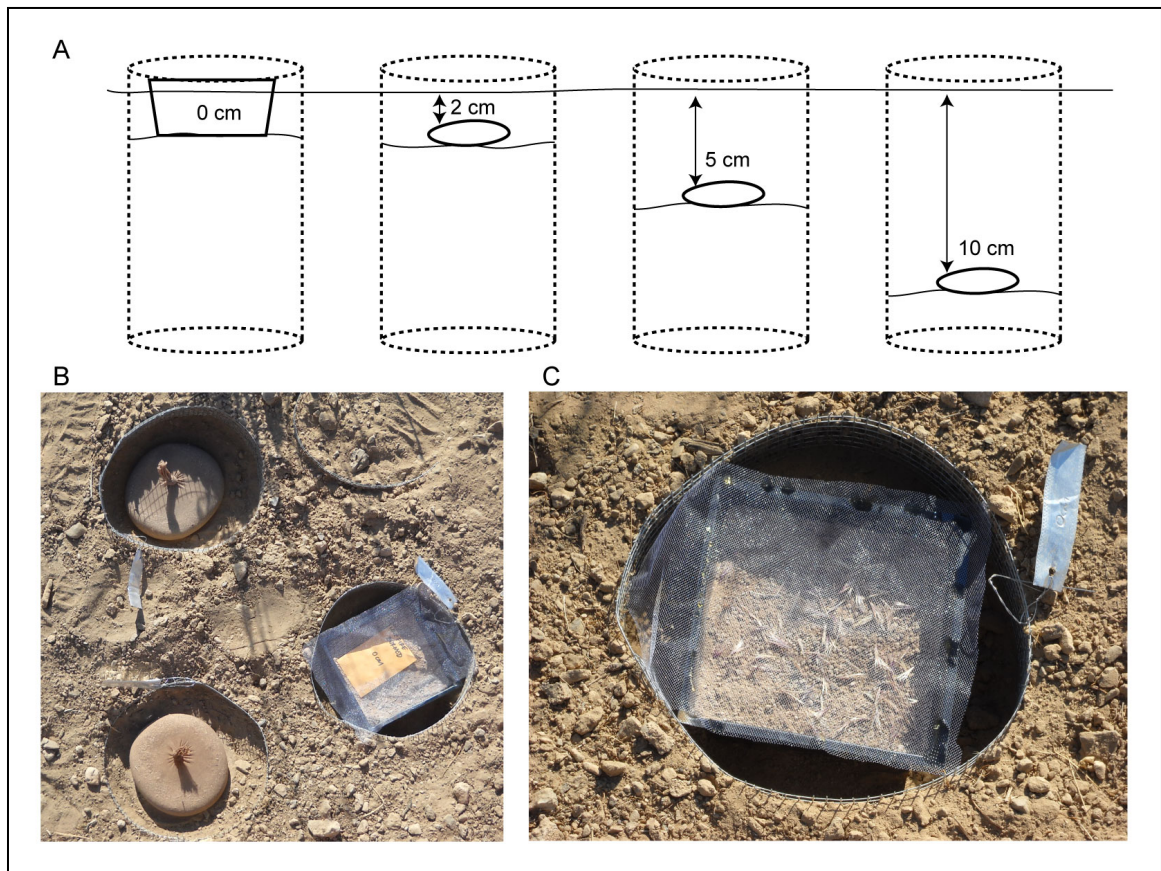


Figure 1. The experimental design featured seed enclosures buried in wire cages at four depths (a). Mesh bags were buried 2, 5, and 10 cm (b). Pots with mesh covers representing surface seeds (0 cm depth) are level with the soil surface (c).

Each seed, once recovered from the enclosure, was inspected under a microscope to determine the condition of the seed. We categorized conditions of each seed in one of two states: viable or nonviable. Viable seeds represent the seeds that have not yet germinated, but still have the potential for germination. These seeds represent the viable

seed bank. Viable seeds had apparently healthy embryos that had not yet germinated. Healthy embryos were firm and did not bend when gently applying pressure with forceps. These seeds also did not have any apparent mold or fungal growth.

Nonviable seeds are no longer part of the viable seed bank because they have either germinated or become damaged or decayed. Seeds that germinate either grow to become seedlings or die before establishing and are effectively removed from the seed bank in the process. Other seeds decay or die before germinating, becoming part of the soil rather than the viable seed bank. Seeds inspected in this study were considered nonviable if they had germinated or were damaged or decayed in the soil. Damaged or decayed seeds did not appear to have a healthy embryo; the embryo was flimsy or brittle when examined with forceps or was not present at all. Damaged or decayed seeds often had confirmed mold or fungal growth. These seeds were dark and shriveled and showed no sign of germination (i.e., no apparent radicle or plumule). Germinated seeds had visual confirmation of radicles and/or plumules emerging from the seed (Figure 2). Depending on how much each seed decayed while buried, plumules were either light green, brown, or dark gray in color.

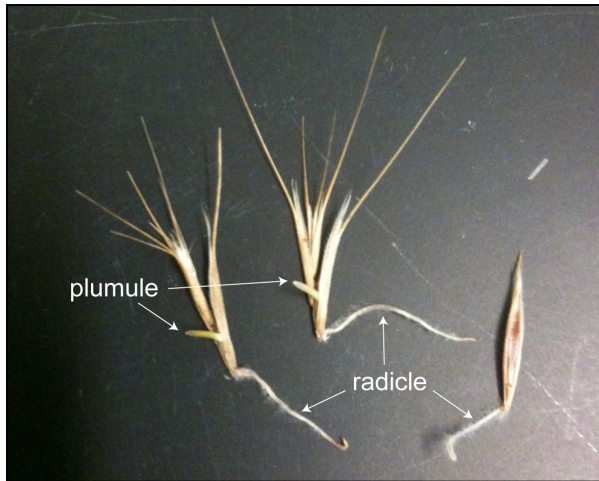


Figure 2. Germinated seeds with confirmed radicles and plumules.

Following the 24-month data recovery, we performed germination trials of recovered seeds, testing a random sampling of 24-month viable and nonviable seeds to determine if germination was still possible. Seeds were placed on filter paper in Petri dishes, given water daily and allowed to germinate. After four days, seeds were checked for signs of germination.

### Data Analysis

The experiment was hierarchically designed with four depth treatments measured at seven recent fires in one burned and one unburned area each. This was repeated four times to accommodate the four durations. We calculated the percentage of seeds viable and nonviable (germinated and decayed) as a proportion of seeds recovered from each seed enclosure. To analyze the data, we used a mixed model analysis of variance (ANOVA) and a generalized linear mixed model (GLMM) with binomial error to accommodate the hierarchical design. The GLMM looked at the main fixed effects of depth, duration, and fire. Seed condition represented the binomial dependent variable with viable seeds representing 'success' and nonviable representing 'failure.' The analysis was completed in SAS v.9.2 (PROC GLIMMIX; SAS Institute, 2002–2008) with the GLMM containing the main fixed effects of burial depth, duration, and fire. Significant effects were compared using Tukey post-hoc tests. Least-squares means and standard errors were back-transformed.

## Study 2: Seed Bank Density and Relationship to Fire

### Study Area

To explore how the composition and density of the soil seed bank responds to burning spatially and temporally, we conducted a seedling emergence study in the greenhouse with samples gathered from the field. Representing a chronosequence spanning 6 to 31 years since fire, we collected soil samples from 12 historic fire sites in

the vicinity of Red Rock Canyon National Conservation Area (Spring Mountains) outside Las Vegas, Nevada. All sites had been previously sampled in burned and unburned interspaces between fertile shrub islands (Engel & Abella, 2011). Sampling and analysis took place between 2008–2010 and included *B. rubens* areal percent cover, soil properties, soil chemistry, and dominant vegetation type for each plot. Engel and Abella (2011) found that successional pathways following fire disturbances in arid environments are driven in large part by community type. To minimize effects on varying successional pathways in different shrub communities, we focused sampling on fires in *Coleogyne ramosissima* (blackbrush) communities only. Unburned sites were dominated by blackbrush. While adjacent burned areas had different species composition (e.g., no blackbrush) when compared to unburned, it was clear that the burn had been in a blackbrush community. Fires occurred between 1980 and 2006, and were grouped for analysis into similar time-fire groups (6–7, 17–19, 24–26, and 29–32 years since burning). All sites were between 1,140 and 1,700 m in elevation. See the Appendix for a map of fire site locations (Figure 11) and description of fire site characteristics (Table 5).

#### Experiment Design

Collection of seed bank samples took place in late fall between November 2 and November 10, 2011, before most winter annual germination occurred in the field (Abella *et al.*, 2009). To compare the possible effects of fire on *B. rubens* seed bank densities, each of the 12 fire sites included samples from burned and unburned areas. Three replicate plots located in the same burned and unburned area were sampled for each fire site, for a total of 72 plots. Soils were sampled at each plot from under shrub canopies and in open interspaces between shrubs to test the effects of fire on seed density and composition in microsites. Three subsamples were collected from under shrub canopies and were combined into one under shrub sample per plot. Each

subsample consisted of 296 cm<sup>3</sup> soil from a 10 cm × 10 cm area and 0–5 cm deep, representing the location of most viable seeds in the seed bank (Abella *et al.*, 2009).

Under-shrub samples were gathered 10 cm from the central stem on the north-facing side of the shrub. We collected soil samples beneath the three closest mature *C. ramosissima* canopies within 10 m of the plot corner location marker. When *C. ramosissima* shrubs were not present—as was often the case in burned areas—we sampled from under the three closest mature native shrub canopies, choosing the dominant species in the immediate area when possible. Other shrub canopies sampled include *Ambrosia dumosa*, *Encelia virginensis*, *Ephedra nevadensis*, *Prunus fasciculata*, *Larrea tridentata*, and *Sphaeralcea ambigua*. Three samples from open interspaces were collected and combined at every plot in the same manner. Interspaces were selected by choosing the three closest bare ground areas at least 1 m from any shrub canopy within 10 m of the plot location marker.

Once collected, samples were brought to the greenhouse at UNLV and were air-dried. A volume of 296 cm<sup>3</sup> from each sample ( $n = 144$ ) was placed atop a mixture of sterile potting soil (Kellogg Garden Products, Carson, CA) and sterile sand (all-purpose sand, supplied by Quikrete, Atlanta, GA). Six control pots were set up with only the sterile potting soil and sand. Due to precipitation that occurred during the field collection, some samples exhibited germination of *B. rubens* and *Erodium cicutarium* before the samples were dried and placed in the pots. As a result, all volumes to be placed in pots were sifted and any germinated seeds were counted and removed. We added these counts to the total emergence for the individual sample pot under the assumption that these seeds would have germinated in pots had they not germinated already.

A total of 150 pots were used for the experiment and were randomly placed in the greenhouse where they were soaked with water for two consecutive minutes every other day using an automatic misting system. Every three weeks, after species identification,

emerging seedlings in each pot were counted and removed from the pots. Additionally, 50 mL of .65 M gibberellic acid was applied to each pot in an effort to spur any seeds that might still be dormant (DeFalco *et al.*, 2009). Total seed bank density was calculated for each species to seeds/m<sup>2</sup> by extrapolating from 296 cm<sup>3</sup> (sample volume) to 50,000 cm<sup>3</sup> (equal to 5 cm depth for 1 m<sup>2</sup>).

### Data Analysis

This study employed a hierarchical nested design where burn year was between subjects (fire sites), burn status (burned or unburned) was within sites, and microsite (under shrub or interspace) was within the plot at each fire site/burn status. The number of seeds that germinated per m<sup>2</sup> for *B. rubens*, *E. cicutarium*, *S. barbatus*, and total natives were analyzed in mixed model analyses of variance (ANOVA). The design was partially hierarchical (Quinn & Keough, 2002), with three fixed effects: burn year assigned among sites (and thus tested over site nested within burn year), burn status assigned within sites (tested over the interaction between burn status and site nested within burn year), and microsite (under shrub and interspace) was assigned within plots (tested over the residual). All two- and three-way interactions among the fixed effects (tested over the residual) were included in the model. The *B. rubens* data met model assumptions after square-root transformation and were tested accordingly. The total natives data were heteroscedastic and had many zeros. Significance was assessed by permuting the data 999 times. *B. rubens*, *E. cicutarium*, and *S. barbatus* data were square-root transformed, analyzed in the ANOVA and tested using permutations. Pairwise contrasts were used to compare significant effects, using normal assumptions or permutations in accordance with the dependent variable. Post-hoc *p*-values were Bonferroni adjusted. For *B. rubens*, back-transformed least-squares means are reported. The means and standard errors for total natives were calculated from 10,000 bootstrap samples (Efron & Tibshirani, 1998). Bootstrap sampling was done in R2.13.0 (R

Development Core Team, 2011); we used SASv9.3 (SAS Institute, 2002-2008) for all other analyses. We used simple linear regression to test for a relationship between *B. rubens* and *Erodium cicutarium* seed densities in microsites of burned and unburned areas.



## CHAPTER 4

### RESULTS

#### Study 1: Seed Longevity

##### Longevity of Red Brome Seeds

There were significant main effects of burial duration and depth, but no interaction between the two (Table 2). Seeds buried six months (mean  $\pm$  standard error: 13.5 percent  $\pm$  1.1 percent) had significantly higher viability than those buried 12 months (6.0 percent  $\pm$  0.9 percent). There was a further reduction in viability at 18 months (1.7 percent  $\pm$  0.5 percent), but no significant difference between 18 months and 24 months (2.6 percent  $\pm$  0.6 percent) (Figure 3a). There was no evidence that fire affected longevity in the soil at any depth or duration (Table 2).

Table 2. Generalized linear model results for viability in the soil as a function of viable and nonviable seeds recovered. Significant values are denoted in bold.

| Effect              | NumDF | DenDF | F     | P             |
|---------------------|-------|-------|-------|---------------|
| FIRE                | 1     | 6     | 0.41  | 0.5437        |
| DURATION            | 3     | 17    | 32.26 | <b>0.0000</b> |
| FIRE*DURATION       | 3     | 17    | 1.51  | 0.2485        |
| DEPTH               | 2     | 12    | 6.78  | <b>0.0107</b> |
| FIRE*DEPTH          | 2     | 12    | 0.16  | 0.8502        |
| DEPTH*DURATION      | 6     | 34    | 1.73  | 0.1437        |
| FIRE*DEPTH*DURATION | 6     | 32    | 0.38  | 0.8831        |

##### Effects of Depth on Red Brome Seeds

Data for seeds placed at 0 cm depths were only collected after the 6-month duration. Beginning with the 12-month duration, most 0 cm pots had either been buried by soil in the surrounding environment, or the mesh had lost integrity, thus contaminating the experimental seeds with seeds from the environment.

Across all burial durations, 7.0 percent  $\pm$  0.9 percent of seeds remained viable at 2 cm depth, a greater proportion of viable seeds than at 5 cm (3.9 percent  $\pm$  0.6 percent) or 10 cm (3.2 percent  $\pm$  0.7 percent) (Figure 3b). When 0 cm data were available for the 6-month duration, 0 cm showed greater proportions of viable seeds (48 percent  $\pm$  8 percent in burned, 43 percent  $\pm$  8 percent in unburned) than any of the other depths after 6-months ( $P < 0.0001$ ) (Figure 4). In Petri dish germination tests of seeds categorized as viable after 24 months, 95 percent of seeds ( $n = 44$ ) had confirmed germination.

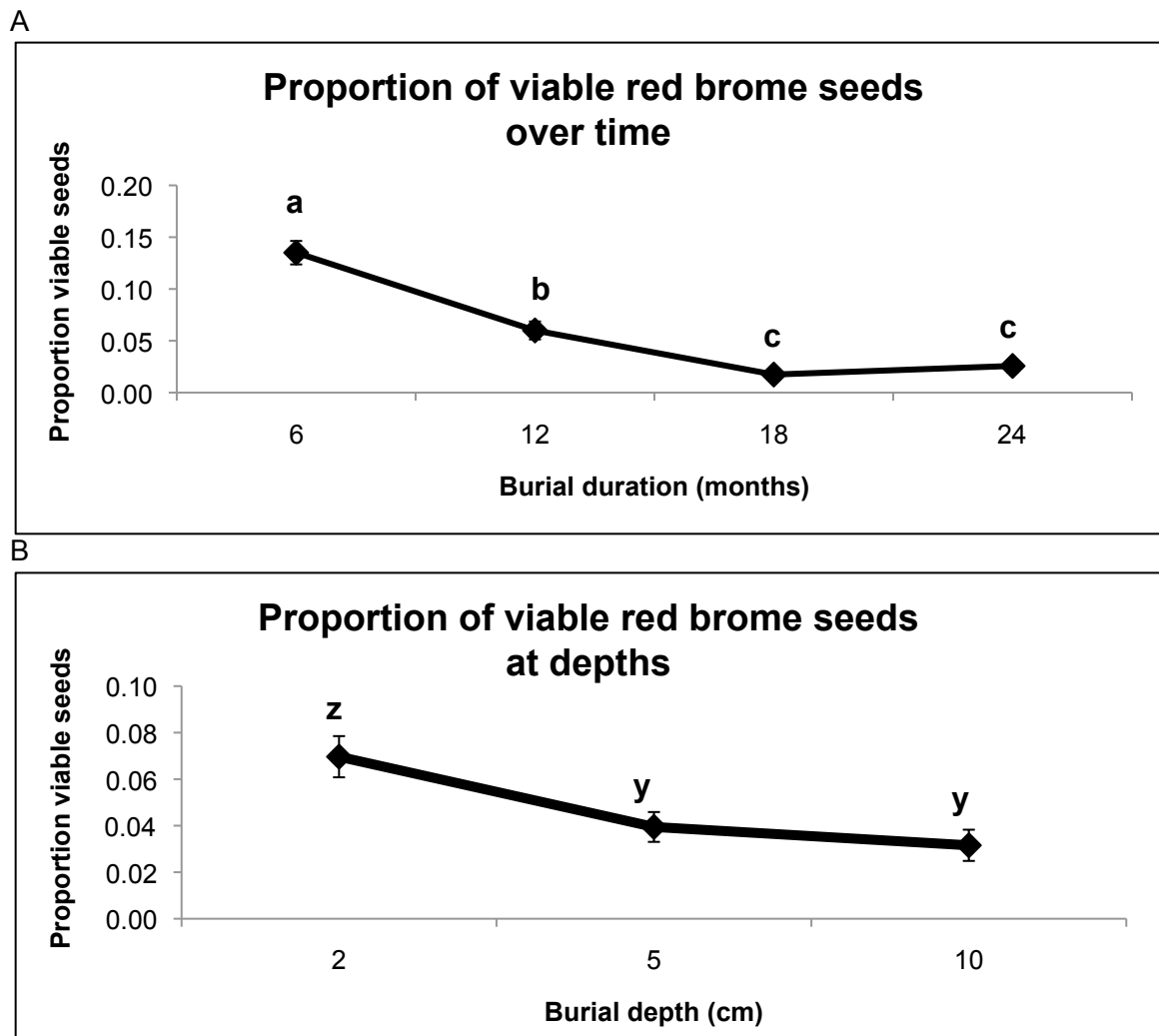


Figure 3. Proportions of viable red brome seeds over time (a; means  $\pm$  S.E.) and at burial depths (b). Seed conditions after 6-month burial had greater proportions of viable seeds than 12 months. Viable seed proportions were further reduced after 18 months and remained low after 24 months. Points sharing letters do not differ ( $P > 0.05$ ).

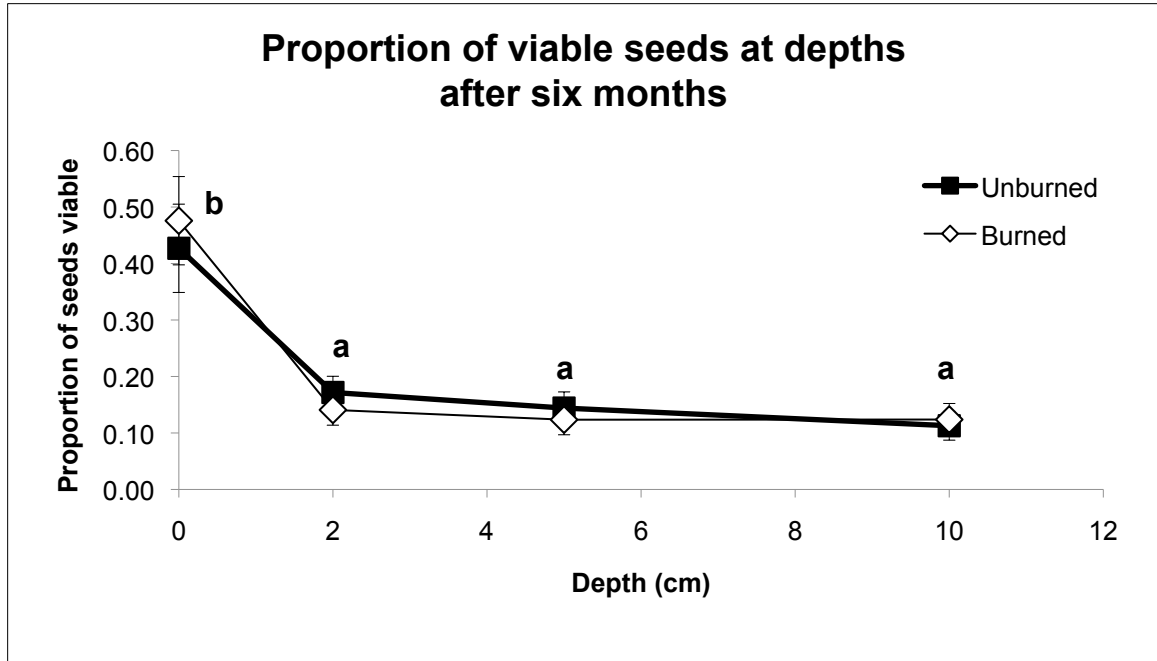


Figure 4. Viable *Bromus rubens* seeds after the 6-month duration at four depths. Points sharing letters do not differ ( $P > 0.05$ ).

## Study 2: Seed Bank Density and Composition Study

### Seed Bank Composition Over Time

In the fire chronosequence study, *B. rubens* was by far the dominant species emerging from seed bank samples in the greenhouse (mean density  $\pm$  standard error:  $5,481 \pm 426$  seeds/m<sup>2</sup>) and was only absent in 5 out of 72 plots. Table 3 describes the full species list and mean densities. Other annual exotic species, *Schismus barbatus* ( $275 \pm 102$  seeds/m<sup>2</sup>) and *Erodium cicutarium* ( $105 \pm 27$  seeds/m<sup>2</sup>), had far less abundant mean densities than *B. rubens* but were respectively the second and third most abundant species in the seed bank samples. Native species mean seed densities were considerably less abundant than any of the exotic species. Ten native species (Table 3) were identified in total, the most abundant of which were the annual *Lepidium lasiocarpum* ( $28 \pm 10$  seeds/m<sup>2</sup>) and annual *Draba cuneifolia* ( $19 \pm 6$  seeds/m<sup>2</sup>).

Table 3. Species emergence and mean densities (seeds/m<sup>2</sup> ± S.E.) for the fire chronosequence study.

| Scientific Name                | Common Name            | Origin | Habit     | Form     | Family         | Mean Density<br>±SE<br>(seeds/m <sup>2</sup> ) |
|--------------------------------|------------------------|--------|-----------|----------|----------------|--|
| <i>Bromus rubens</i>           | red brome              | Exotic | Annual    | Grass    | Poaceae        | 5,481 ±426                                     |
| <i>Erodium cicutarium</i>      | redstem filaree        | Exotic | Annual    | Forb     | Geraniaceae    | 105 ±27  |
| <i>Schismus barbatus</i>       | schismus grass         | Exotic | Annual    | Grass    | Poaceae        | 275 ±102                                       |
| <i>Cryptantha</i> spp.         | cryptantha             | Native | Annual    | Forb     | Boraginaceae   | 2 ±2   |
| <i>Descurainia pinnata</i>     | tansy mustard          | Native | Annual    | Forb     | Brassicaceae   | 6 ±3   |
| <i>Draba cuneifolia</i>        | wedgeleaf draba        | Native | Annual    | Forb     | Brassicaceae   | 19 ±6  |
| <i>Lepidium lasiocarpum</i>    | shaggyfruit pepperweed | Native | Annual    | Forb     | Brassicaceae   | 28 ±10   |
| <i>Plantago ovata</i>          | indianwheat            | Native | Annual    | Shrub    | Plantaginaceae | 6 ±3   |
| <i>Astragalus</i> spp.         | milkvetch              | Native | Perennial | Forb     | Fabaceae       | 5 ±2   |
| <i>Baileya multiradiata</i>    | desert marigold        | Native | Perennial | Forb     | Asteraceae     | 1 ±1   |
| <i>Encelia</i> spp.            | brittlebrush           | Native | Perennial | Shrub    | Asteraceae     | 6 ±3   |
| <i>Sphaeralcea ambigua</i>     | globemallow            | Native | Perennial | Forb     | Malvaceae      | 5 ±2   |
| <i>Thymophylla pentachaeta</i> | fiveneedle pricklyleaf | Native | Perennial | Subshrub | Asteraceae     | 3 ±2   |

Time-since-fire groups showed no differences in *B. rubens* seed density, nor was there an effect of time-since-fire on natives. However, the other exotic annual species identified in the study were most abundant in specific time-since-fire groupings. *S. barbatus* had the greatest seed densities in the youngest time-since-fire group (6–7 years) ( $P = 0.021$ ), while *E. cicutarium* had the greatest densities in the intermediate time-since-fire group (17–19 years) ( $P = 0.043$ ).

### Red Brome Post-Fire Seed Bank Densities

There was not a significant effect of burn status (burned or unburned) on *B. rubens* seed bank densities. However, *B. rubens* seed density was less abundant in unburned interspaces than burned interspaces and under shrubs in either burned or unburned areas (Table 4, Figure 5,  $P = 0.017$ ,  $F = 6.5$ ).

Table 4. ANOVA results showing fixed effects of burn status, microsite, and time-since-fire interactions for seed densities of *Bromus rubens*, *Erodium cicutarium*, *Schismus barbatus*, and native species. Significant values are denoted in bold.

| Variable/Effect                        | <i>Bromus rubens</i> |              | Native species |              | <i>Erodium cicutarium</i> |              | <i>Schismus barbatus</i> |              |
|--|----------------------|--------------|----------------|--------------|---------------------------|--------------|--------------------------|--------------|
|  | $\eta^2$             | Permuted P   | $\eta^2$       | Permuted P   | $\eta^2$                  | Permuted P   | $\eta^2$                 | Permuted P   |
| BURN (burned, unburned) <sup>1,3</sup> | 10.6                 | <b>0.003</b> | 0.1            | 0.783        | 14.2                      | <b>0.001</b> | 0.1                      | 0.753        |
| BURN*MICROSITE <sup>1,4</sup>          | 6.5                  | <b>0.017</b> | 1.1            | 0.300        | 0.2                       | 0.678        | 1.7                      | 0.214        |
| MICROSITE <sup>1,4</sup>               | 17.4                 | <b>0.001</b> | 8.3            | <b>0.002</b> | 1.2                       | 0.305        | 0.0                      | 0.879        |
| TSF (time-since-fire) <sup>2,3</sup>   | 0.7                  | 0.508        | 0.5            | 0.679        | 2.4                       | <b>0.043</b> | 0.9                      | 0.383        |
| TSF*BURN <sup>2,3</sup>                | 1.4                  | 0.219        | 1.1            | 0.329        | 2.2                       | 0.090        | 0.5                      | 0.689        |
| TSF*BURN*MICROSITE <sup>2,4</sup>      | 0.5                  | 0.664        | 1.1            | 0.382        | 0.2                       | 0.915        | 3.4                      | <b>0.021</b> |
| TSF*MICROSITE <sup>2,4</sup>           | 8.5                  | <b>0.001</b> | 1.3            | 0.309        | 7.1                       | <b>0.002</b> | 0.6                      | 0.662        |

<sup>1</sup> NumDF=1, <sup>2</sup> NumDF=3, <sup>3</sup> DenDF=8, <sup>4</sup> DenDF=112

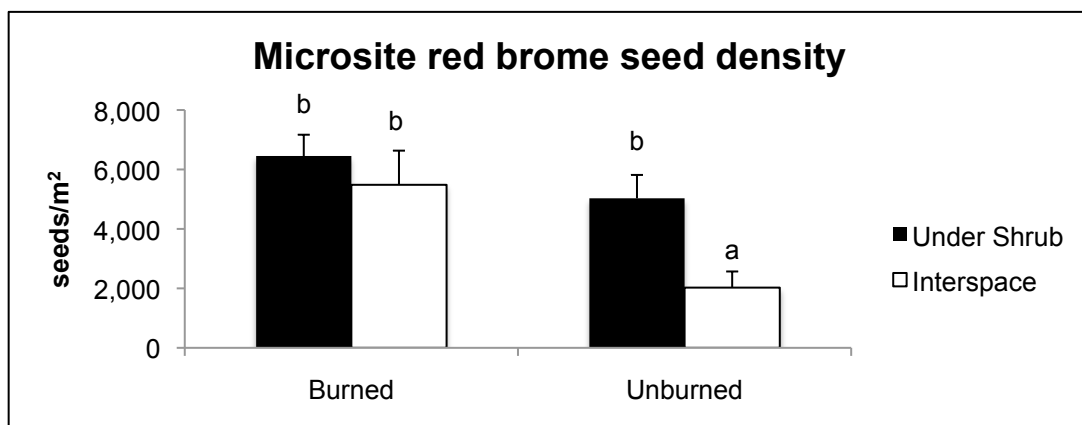


Figure 5. Comparison of *Bromus rubens* seed density between microsites in burned and unburned areas. Unburned interspaces have significantly lower seed density than unburned under shrubs and both burned microsites. Bars sharing letters do not differ ( $P > 0.05$ ).

For most of the time-since-fire groups, there were greater *B. rubens* seed densities under shrubs than in interspaces (Figure 6). This was true in the youngest fires (6–7 years since burning) and the oldest fires (24–26 and 29–32 years, respectively). The pattern in intermediate years (17–19 years) was qualitatively reversed and not statistically significant after the Bonferroni correction. The same time-since-fire group (17–19 years) had greater *B. rubens* seed densities in burned interspaces than unburned interspaces (Figure 7a). Burn effects were not statistically significant in other time-since-fire groupings, but there was a trend toward greater seed densities in burned interspaces than unburned interspaces. Under shrubs there were no patterns of burning or time-since-fire on seed bank density (Figure 7b).

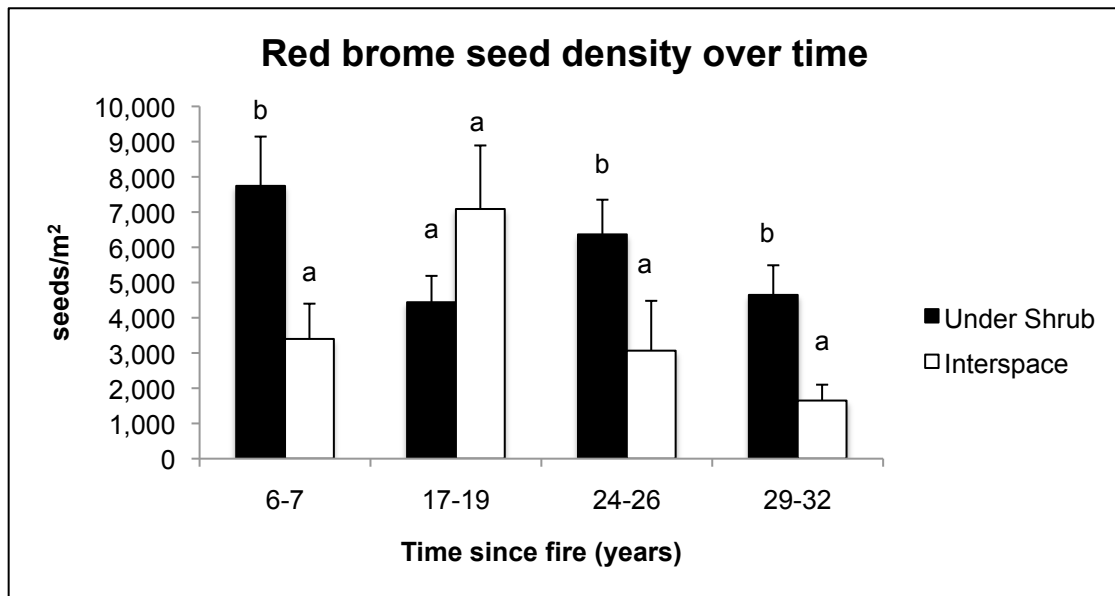


Figure 6. Microsite effects on *Bromus rubens* seed density. Seed densities under shrubs were greater than in interspaces for three of the four time-fire groupings. Bars sharing letters do not differ ( $P > 0.05$ ).

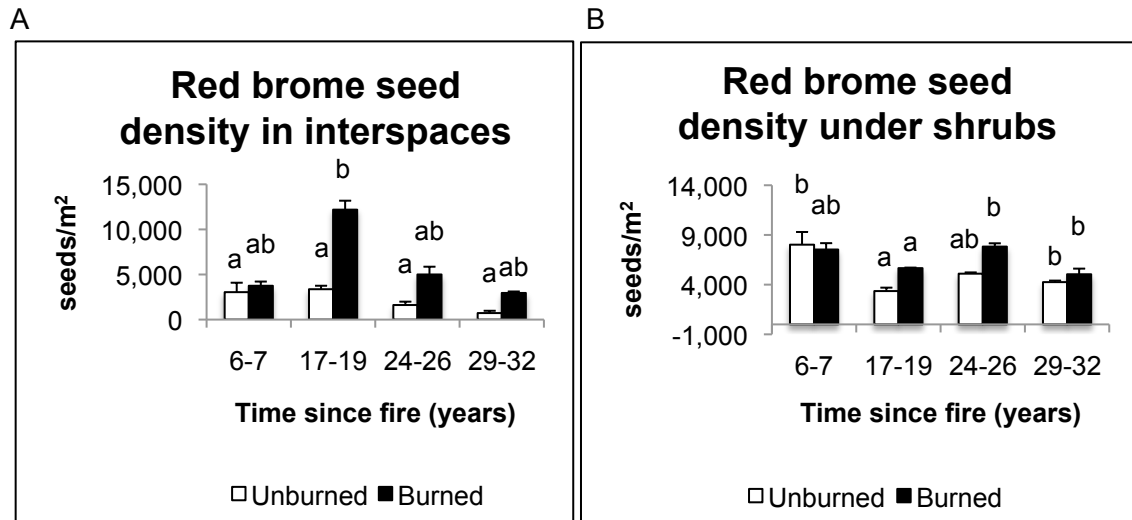


Figure 7. *Bromus rubens* seed bank density within interspaces (a) and under shrubs (b; means  $\pm$  S.E.). Bars sharing letters do not differ ( $P > 0.05$ ).

#### Seed Bank Density of Other Species

There was no difference in native seed density between burned and unburned plots. While native seed densities were not affected by fire, they were influenced by microsite and were greater under shrubs than in interspaces ( $P = 0.002$ ; Figure 8b). The exotic annual species *E. cicutarium* was the only species in the study to have greater seed densities in burned as compared to unburned plots ( $P = 0.001$ ; Figure 8a). However, the majority of *E. cicutarium* seedlings emerged from samples in the intermediate time grouping (17–19 years). When compared to *B. rubens* densities in the same time grouping (17–19 years), there was a positive relationship ( $P = 0.006$ ,  $R^2 = 0.681$ ) between *B. rubens* and *E. cicutarium* seed densities in burned interspaces (Figure 9).

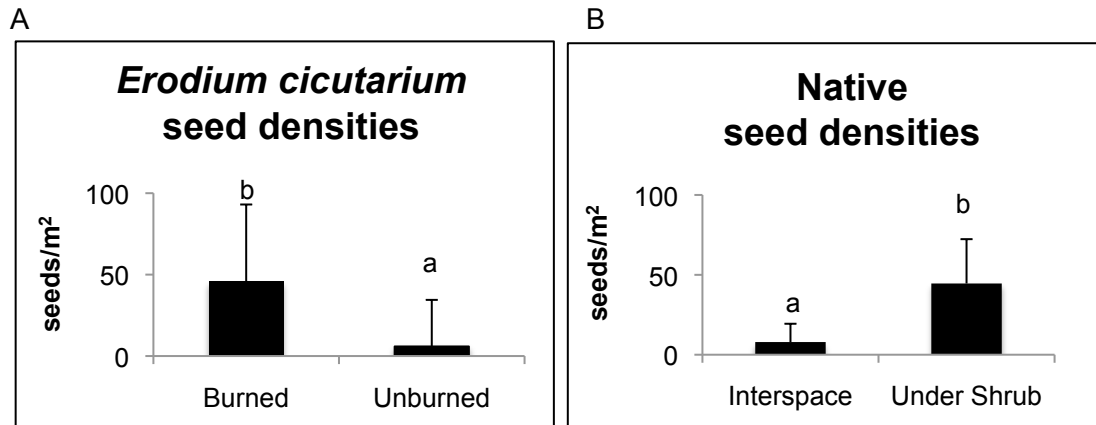


Figure 8. Comparison of seed densities of (a) *Erodium cicutarium* between burned and unburned areas and (b) native species between microsites. Letters denote significant differences among means ( $P < 0.05$ ).

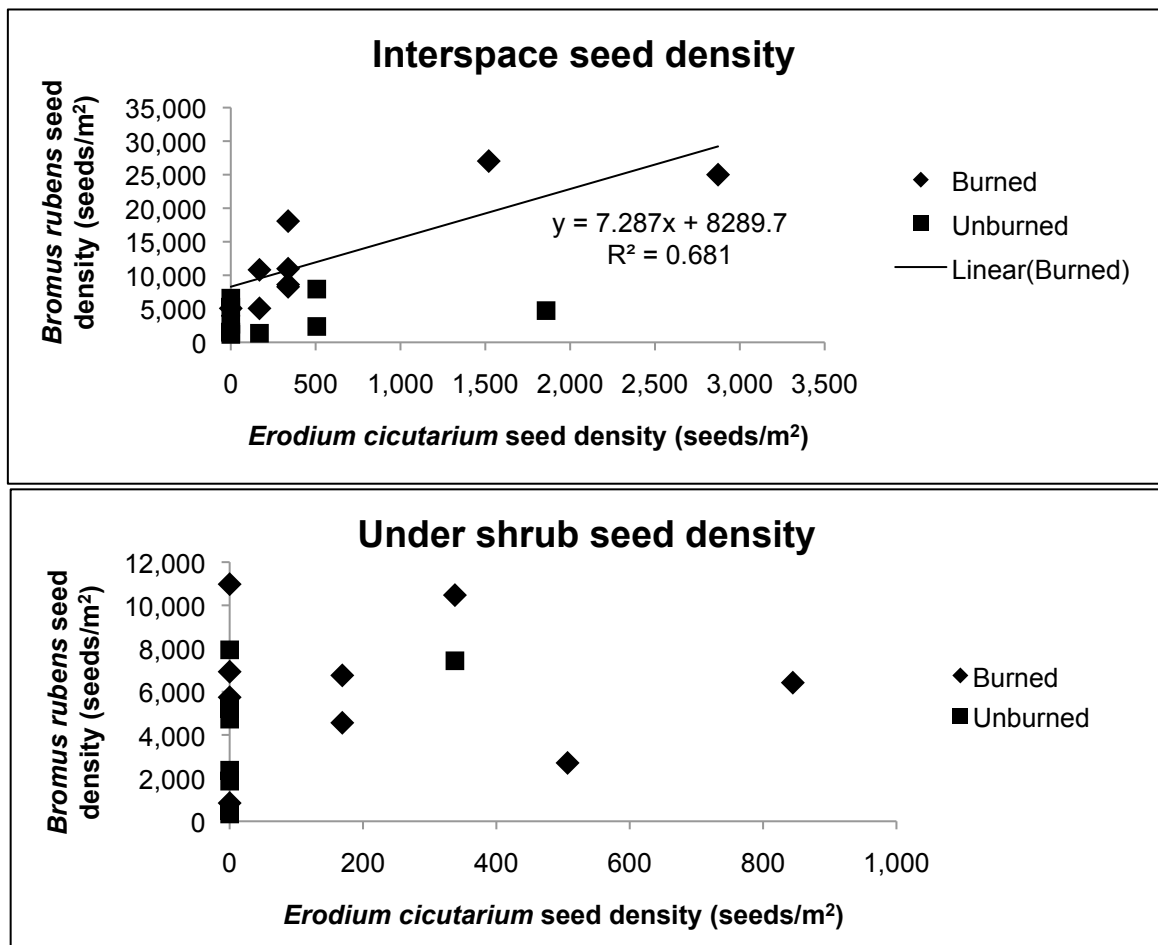


Figure 9. Linear regression of *Bromus rubens* and *Erodium cicutarium* seed densities in interspaces and under shrubs in the second youngest time-since-fire group (17–19 years since fire). In burned interspaces, the two species were positively related ( $R^2 = 0.681$ ).



## CHAPTER 5

### DISCUSSION

#### Study 1: Seed Longevity

##### Longevity of Red Brome Seeds

The proportion of viable seeds in the soil was greatly reduced over time, matching our predictions. We found a greater proportion of viable seeds (6.0 percent  $\pm$  0.9 percent) after twelve months than Wu and Jain's (1979) estimate of 2 percent carry-over each year. This suggests that, while still a small proportion, as many as two or three times more seeds can carry-over to the next year than has previously been reported. Additionally, while proportions of viable seeds are significantly reduced after 18 months, there was still a fraction remaining viable after 24 months (Figure 10). This finding concurs with Brooks' (2000) estimate that some red brome seeds can remain viable in the soil for at least two years. That we were able to germinate viable seeds after 24-month duration confirms that buried seeds can germinate even two years after being introduced to the soil seed bank.

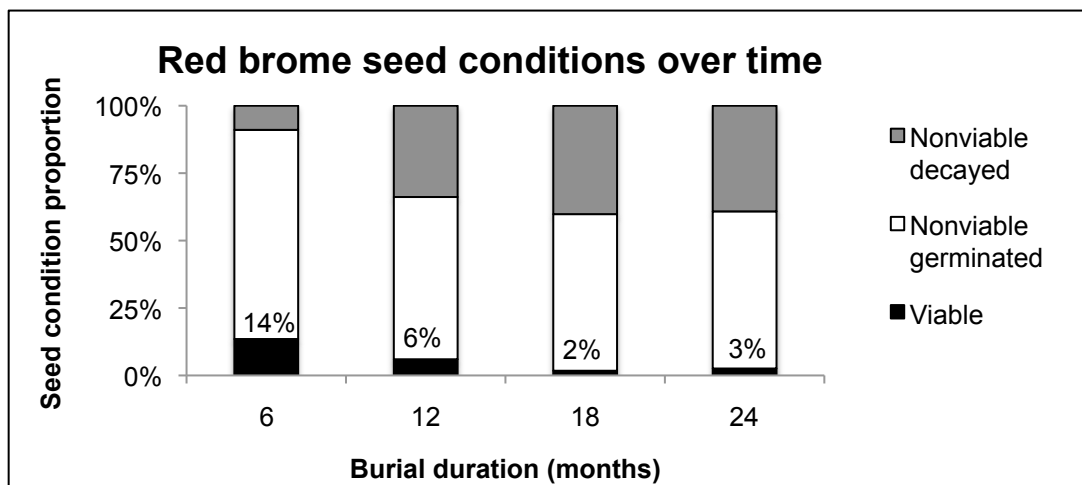


Figure 10. Proportions of nonviable (decayed and germinated) and viable red brome seeds after all burial durations.

Our findings indicate similar first-year carry-over of seeds to Smith *et al.*'s (2008) findings for *B. tectorum*, reporting between 7.6 percent and 9.3 percent carry-over in the first year for *B. tectorum* as compared to approximately 6 percent for *B. rubens* in our study. However, after two years, viable cheatgrass seeds were reduced considerably more than red brome. This may be the result of differences in experimental design as Smith *et al.* (2008) tested the effects of different levels of seed rain (dispersal of seeds into the soil seed bank), whereas our design featured a fixed number of seeds manually buried. This difference in viability after two years may also be the result of differences in climate between ranges of *B. rubens* and *B. tectorum*. Our results also suggest that the slow rebound of populations of *B. rubens* after a fire event or population crash due to drought may be related in part to the large depletion of viable seeds in the seed bank after one or two years. This supports the notion that most seeds in rebounding populations of red brome are often due to seed dispersal from neighboring areas rather than emerging from the soil, however it does not preclude the possibility.

#### Effects of Depth on Red Brome Seeds

When looking at the effects of burial depth, our results coincide with results from Abella *et al.* (2011) in which seedling emergence was shown to decrease with burial depth, *B. rubens* seed viability also declined with greater burial depths. Viable seed proportions were significantly lower at 5 and 10 cm than at 2 cm across all burial durations. This reduction in viability due to burial depth also concurs with those of other brome species (Jensen, 2008; Narwal *et al.*, 2008) and may be the result of factors such as differences in light penetration, soil oxygen, moisture, or temperature. Following the 6-month duration there were significantly more viable seeds on the surface (0 cm) than were buried at any depth, suggesting that seeds covered with soil are less likely to remain viable, concurring with Gleichsner and Appleby (1989).

### Effect of Fire on Red Brome Seeds

The hypothesis that there would not be a great difference between seeds from areas burned and unburned was also confirmed. Further testing of burial durations would help our understanding as it relates to the proportions of dormant seeds of red brome after three or five years. Additionally, future studies could focus on how the dynamics of viable seeds change at the surface (0 cm) as compared to buried seeds.

### Summary

The results of this study confirm many assumptions about the seed dynamics of *B. rubens*. We confirmed that a small portion of seeds remain viable for at least two years in the soil. Additionally, larger proportions of seeds lose their viability at greater burial depths. We found a greater proportion of viable seeds are carried-over to the next year than previously thought, but still found viability substantially reduced between six months and one year. With a better understanding of how long and to what extent *B. rubens* seeds remain viable in the soil over time, this information may help inform management strategies to control the spread and impact of this invasive species in the native ecosystems of the Mojave Desert. *B. rubens* does not appear to have long-term viable seed banks as do many native desert annuals.

## Study 2: Seed Bank Density and Composition Study

### Seed Bank Composition Over Time

This study confirmed that when red brome is a major component of above-ground vegetation it dominates the desert soil seed bank, even in the youngest fires sampled (six years since fire). Overall, *B. rubens* seed density patterns varied greatly between sites (Appendix Figure 12), but the species was considerably more abundant than any other. While the other exotic species did have greater seed densities in certain time-since-fire groups, there was not a clear trend over time, suggesting that these

differences were more likely due to site variation rather than any process influenced by time. Therefore, there was no support for the hypothesis that there is a relationship between the amount of time since burning and seed bank densities. This suggests that time-since-fire does not influence the seed densities of red brome or natives, at least in the time horizon studied (6–31 years since fire).

However, when comparing our results to Abella *et al.* (2009), who sampled fires two years after burning, we found much different patterns an additional four years (or six years total) since fire. Where they reported greater seed densities in burned interspaces than burned under shrubs two years after fire, we found the reverse pattern six years after burning. In our 6–7 year samples, there were significantly greater seed densities under shrubs than interspaces on burned areas (Figure 6). Additionally, Abella *et al.* (2009) observed greater *B. rubens* seed densities in burned than unburned areas under dead, charred individuals. While we sampled under live individuals, only four years later, we found burned and unburned seed densities were generally more alike, supporting Brooks' (2002) observations that red brome rebounds quickly as indicated by the four-year window between Abella *et al.*'s (2009) sampling and this study. This suggests that, in general, *B. rubens* densities quickly rebound to form similar seed densities between burned and unburned areas, with greater seed densities tending to be under shrubs rather than in open interspaces. This was certainly the most common outcome among time-since-fire groups.

#### Red Brome Post-Fire Seed Bank Densities

Soil seed bank density patterns of red brome were spatially variable across the 31-year time-since-fire chronosequence, and generally were not related to burn status. Only the 17–19 year fires showed any significant differences between burned and unburned. The other three time-since-fire groups (youngest and oldest) had similar results: while there was no effect due to burn status, there were significantly greater *B. rubens* seed

densities under shrubs than in interspaces. This concurs with observed patterns of greater *B. rubens* cover densities under shrub canopies than in the interspaces (D'Antonio & Vitousek, 1992). It does not support the hypothesis that there would be less difference in seed densities between microsites on burned and unburned areas over time, as this was not observed in most time-since-fire groups.

This is not the case on all fire sites, however. In the 17–19 years since fire group, *B. rubens* seed densities were significantly greater in burned interspaces than unburned interspaces. Two fires largely drove this significance in this time-since-fire group: the Blue Diamond Mine fire (1993, 19 years since burning) and the Willow fire (1995, 17 years) (Appendix Figure 12). In other time-since-fire groups, we observed marginally greater seed densities in burned interspaces than unburned, but this was not statistically significant. Without further exploration of these sites, it is difficult to know what may be responsible for the greater *B. rubens* seed densities in burned interspaces in the 17–19 years since fire group.

Greater *B. rubens* seed densities in interspaces as a result of burning supports the grass-fire theory that burned areas promote greater red brome seed density in interspaces (Rao *et al.*, 2010), likely increasing the seedling emergence and above-ground cover. Altered spatial patterns reflected in greater densities of red brome seeds in interspaces enable greater connectivity of fuels for wildfires (Salo, 2004). However, this notion is not strongly supported by the results of this study, as it only occurred in a portion of the sites sampled. Where altered patterns were observed (e.g., on the Blue Diamond Mine and Willow fires), it is unclear what conditions may have affected the significantly greater seed densities in burned interspaces when compared to unburned.

Species composition can vary greatly between burned and unburned areas after a fire (Engel & Abella, 2011), as we observed at all of the 12 fire sites in this study. Many of the shrubs we sampled under were early-successional species such as *Sphaeralcea*

*ambigua* and were not paired with the samples under the same species in unburned areas. However, seed densities were far less variable under shrub canopies between burned and unburned areas than was observed in interspaces. This indicates that overall under shrub canopies of multiple species can have similar densities of red brome seeds.

#### Seed Bank Density of Other Species

Interestingly, the same time-since-fire group (17–19 years) also had notably different patterns in seed densities of *E. cicutarium* in burned interspaces than the other three time-since-fire groups. It was also the species to show the clearest relationship to burn status, with far greater seed densities in burned than unburned areas (Figure 8a). This concurs with previous findings that *E. cicutarium* increases rapidly in burned areas following fire (Abella, 2010). *B. rubens* and *E. cicutarium* seed densities were positively correlated ( $R^2 = 0.681$ ) in the interspaces of the 17–19 years since fire group. This suggests that the presence of *E. cicutarium* relates to *B. rubens* seed densities (or vice versa) in burned interspaces. While it is difficult to draw substantial conclusions from these results, further investigation of this relationship may help identify how *E. cicutarium* and *B. rubens* seed densities relate to one another ecologically in interspaces.

In burned areas, *S. barbatus* seed densities were marginally increased over unburned areas, but its presence at all sites was variable. It was mostly found in the youngest fires, which could suggest that earlier post-fire conditions may benefit *S. barbatus*. Both *E. cicutarium* and *S. barbatus* had far less emergence in the greenhouse and were absent from many plots. Therefore, the plots where these exotics did emerge drove the patterns. Natives did not appear to be affected by burning at all, which did not support the hypothesis that native seed densities can be reduced in burned areas. Native densities in the seed bank did not change in burned areas over time, either. The composition of native species was highly variable, however, as was expected.

## Summary

Overall, in the fires sampled, red brome seed densities were not affected by time in the chronosequence spanning 6–31 years since fire. Seed densities of *B. rubens* were variable and showed no clear pattern that applied to all sites. The other exotic species identified were more affected by burning than was *B. rubens*, but were also far less abundant. The fires that showed reverse patterns in microsites with greater *B. rubens* seed densities in interspaces than under shrubs were likely different due to variations between the sites, rather than the amount of time that passed since burning. The greater densities of *E. cicutarium* in interspaces in these sites may suggest a relationship to *B. rubens* and warrants further investigation. Native seed densities for the species we identified were not impacted by fire or by the presence of red brome.

*B. rubens* dominated the samples we tested in the greenhouse. That seed densities were not affected by fire in all cases suggests there is little direct impact due to burning in as little as six years after the fire. Seed bank densities were not significantly different between burned and unburned. As related to the grass-fire theory, where the burned areas may not have been favoring brome over unburned areas, it is clear that brome re-colonized burned areas quickly and formed prolific seed banks. While fire does not necessarily promote greater seed densities of red brome in burned areas, it is clear that the window of opportunity for managers to engage in revegetation of native species is small indeed, as even fires six years after burning showed little difference between burned and unburned areas.

## Further Research

This research explored several untested aspects of the seed bank characteristics of red brome. Further research will address the longevity of red brome seeds beyond two years, as the seed enclosure design included two longer burial duration treatments.

Seed enclosures are presently in the field to test the longevity of seeds after 4.5 and seven years in the soil. This will likely give us the full picture of how long seeds remain viable in the seed bank.

Future sampling and analysis of the fire sites sampled in Study 2 for above-ground cover and composition of species present will connect what we found in the soil seed bank with what is growing in the environment. Identifying what factors influence the increase of red brome in the burned interspaces (such as relationships to *E. cicutarium*) may improve our understanding of what facilitates the spread of the species. Challenges remain to addressing the spread of *B. rubens* in the Mojave, but gaining a better understanding of the structure of seed banks contributes valuable information to assist in future management strategies.



## APPENDIX

Table 5. Fire site characteristics

| Burn Year | Fire Name                    | Elevation (m) | Soil Texture | pH   | Total Org. C (%) | Total N (%) |
|-----------|------------------------------|---------------|--------------|------|------------------|-------------|
| 2005      | Loop (burned)                | 1,248         | Sandy loam   | 7.28 | 1.20             | 0.08        |
| 2005      | Loop (unburned)              | 1,284         | Loam         | 7.25 | 1.01             | 0.06        |
| 2005      | 2005 Red Rock (burned)       | 1,179         | Sandy loam   | 7.07 | 0.58             | 0.02        |
| 2005      | 2005 Red Rock (unburned)     | 1,180         | Loamy sand   | 7.24 | 0.36             | 0.02        |
| 2006      | Scenic (burned)              | 1,170         | Sandy loam   | 7.11 | 0.42             | 0.04        |
| 2006      | Scenic (unburned)            | 1,179         | Loamy sand   | 6.92 | 0.22             | 0.02        |
| 1993      | 1993 Red Rock (burned)       | 1,319         | Sandy loam   | 7.42 | 1.57             | 0.07        |
| 1993      | 1993 Red Rock (unburned)     | 1,339         | Sandy loam   | 7.52 | 1.48             | 0.03        |
| 1993      | Blue Diamond Mine (burned)   | 1,140         | Loamy sand   | 7.21 | 2.11             | 0.06        |
| 1993      | Blue Diamond Mine (unburned) | 1,140         | Loamy sand   | 7.57 | 0.39             | 0.04        |
| 1995      | Willow (burned)              | 1,352         | Sandy loam   | 7.29 | 2.85             | 0.13        |
| 1995      | Willow (unburned)            | 1,466         | Sandy loam   | 7.45 | 1.64             | 0.11        |
| 1986      | K389 (burned)                | 1,370         | Sandy loam   | 7.47 | 1.52             | 0.16        |
| 1986      | K389 (unburned)              | 1,384         | Sandy loam   | 7.62 | 1.92             | 0.09        |
| 1988      | Sterling (burned)            | 1,686         | Sandy loam   | 7.32 | 1.42             | 0.10        |
| 1988      | Sterling (unburned)          | 1,659         | Sandy loam   | 7.50 | 0.81             | 0.08        |
| 1988      | Zipper (burned)              | 1,504         | Sandy loam   | 7.67 | 0.91             | 0.07        |
| 1988      | Zipper (unburned)            | 1,473         | Sandy loam   | 7.58 | 0.86             | 0.06        |
| 1983      | 4322 Red Rock (burned)       | 1,211         | Loamy sand   | 7.23 | 0.51             | 0.05        |
| 1983      | 4322 Red Rock (unburned)     | 1,208         | Sand         | 7.03 | 0.42             | 0.04        |
| 1980      | Cottonwood (burned)          | 1,405         | Sandy loam   | 7.11 | 2.61             | 0.20        |
| 1980      | Cottonwood (unburned)        | 1,339         | Sandy loam   | 7.49 | 1.69             | 0.04        |
| 1980      | SR160-Hillside (burned)      | 1,638         | Sandy loam   | 7.20 | 2.60             | 0.19        |
| 1980      | SR160-Hillside (unburned)    | 1,559         | Sandy loam   | 7.13 | 1.80             | 0.13        |

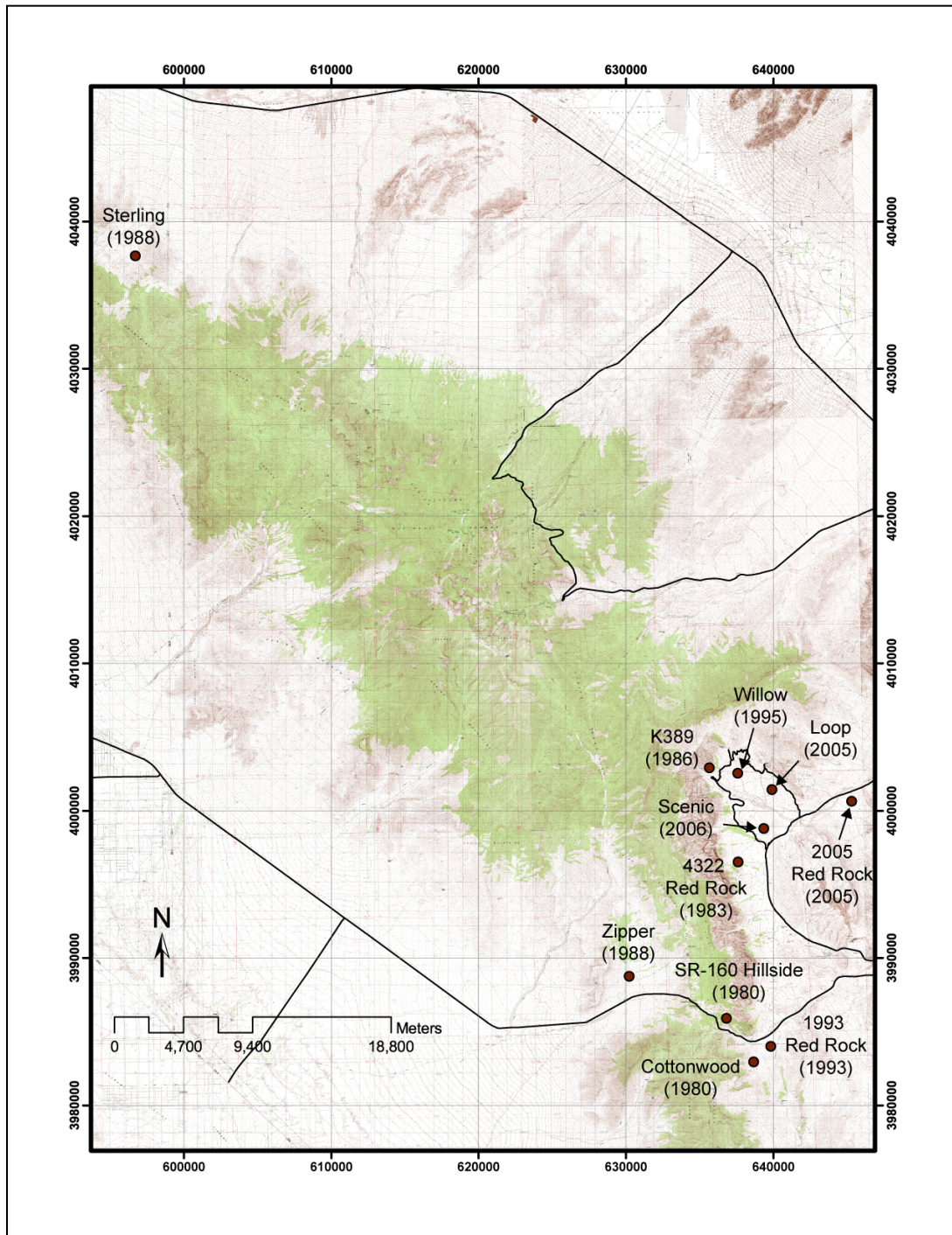
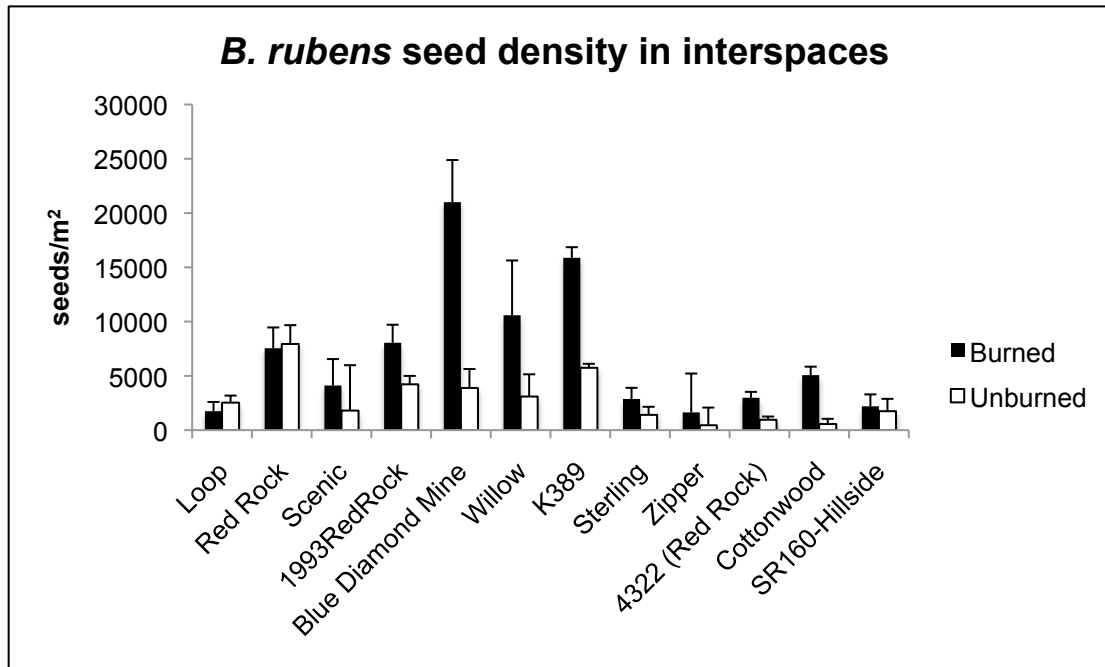


Figure 11. Fire site locations for Study 2; fire names given with year of fire.

A



B

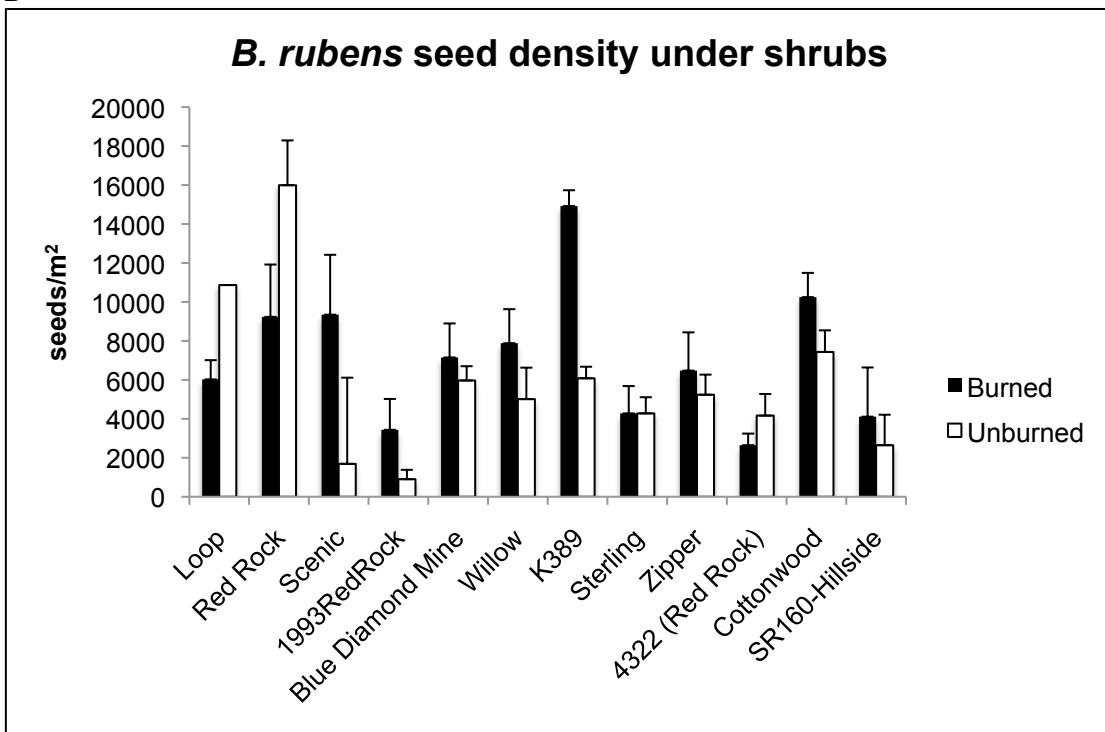


Figure 12. *Bromus rubens* seed densities by fire site in interspaces (a) and under shrubs (b; means  $\pm$  S.E.). Differences between burned and unburned were variable, indicating no clear pattern in seed densities as the result of burning.

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Exploring the seed bank dynamics of red brome: Longevity, density, and relationship to fire

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