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Soil seed bank longevity of the exotic annual grass *Bromus rubens* in the Mojave Desert, USA

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ABSTRACT

Although arid environments are often considered among the least invaded terrestrial biomes, the impacts of exotic plant species can be severe and long lasting. *Bromus rubens* (red brome) is an exotic annual grass species in the Mojave Desert known to outcompete native plant species, alter habitat, and promote accumulation of fuel that contributes to increasing fire frequency and severity. We assessed longevity of the exotic *B. rubens* seeds in the soil by burying seeds at four depths (0, 2, 5, and 10 cm) and recovering seeds 6, 12, 18, and 24 months after burial. Seed viability was reduced with greater burial depth and greater time since burial. A relatively small proportion of seeds retained viability for two years, suggesting that while the *B. rubens* seed bank can be large, it is relatively short-lived. Although *B. rubens* apparently relies more on the annual production, dispersal, and germination of seeds than on a long-lived seed bank for its annual recruitment, the numerous seeds produced by individual plants indicate that even a small proportion of seeds remaining viable for more than a year can aid recruitment from the seed bank and is an important factor in understanding population dynamics.

1. Introduction

Annual plant species often comprise a large portion of desert floras and have adapted seed bank and recruitment strategies in response to the variable precipitation, temperature extremes, and fluctuating plant-available nutrients of arid environments (Guo et al., 1998, 1999). The longevity of seeds in the surface soil varies greatly among annual species (Saatkamp et al., 2009). Some annual species produce seeds that remain viable in the soil over multiple years, while others produce short-lived seeds that may only be viable for a single season (Baskin and Baskin, 2001). By maintaining a portion of viable seeds that persist in the soil across multiple seasons, many desert annual plant species can be sustained even through drought (Esque et al., 2010; Salo, 2004; Venable et al., 1993). In contrast, some annual grass species have features (such as awns) that anchor seeds in the soil where they can germinate quickly, resulting in transient seed banks that generally survive less than one year (Bekker et al., 1998). Once in the soil, a seed may germinate, die before germinating (e.g., through predation, aging, or damage), or remain viable and ungerminated in the soil over a period of time (Baskin and Baskin, 2001). The longevity of viable seeds in the soil over time can be the result of dormancy—morphological or physical—or a lack of adequate available moisture, temperatures, and other triggers conducive to germination (Baskin and Baskin, 2001).

Although deserts are often considered among the least invaded ecosystems (Brooks, 2003), they can be significantly impacted by exotic species having long-lasting consequences to native plant communities. With the introduction and spread of exotic species, seed banks can be dramatically altered and in many cases become dominated by exotic species (Cox and Allen, 2008; DeFalco et al., 2009; Espeland et al., 2010; Esque et al., 2010; Schneider and Allen, 2012). Not only can exotic species alter seed banks and outcompete native species, they can also modify ecosystem structure and function (Reid et al., 2006). For example, the introduction of exotic annual grass species into novel habitats has altered fire regimes around the world, as is the case with *Hyparrhenia rufa* and *Melinis minutiflora* in Central and South America, and *Pennisetum polystachyon* in the arid lands of Australia (D'Antonio and Vitousek, 1992). In the southwestern United States, invasion of annual grass species has corresponded with increases in the frequency, size, and severity of wildfires that can convert native shrub communities to exotic annual grasslands. *Bromus rubens* (red brome; hereafter, *Bromus*) is one such exotic species that has greatly impacted southwestern US arid lands

Abbreviations: GLMM, Generalized linear mixed model; RRCNCA, Red Rock Canyon National Recreation Area.

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by contributing continuous-cover fine fuels that promote wildfires in formerly fuel-limited deserts (Brooks, 2009). These fires dramatically alter native species composition, converting late-successional communities of long-lived perennial shrubs to dominance by shorter-lived species (Abella, 2009; Brooks and Chambers, 2011).

Wildfires fueled by *Bromus* and other exotic grass species in deserts can change soil properties, alter plant community composition, and impact seed banks. Temperatures during fires can vary, as Patten and Cave (1984) observed in Sonoran Desert uplands where temperatures were greater under shrubs (210 °C) than in open interspaces (60 °C). Annual plant and seed bank densities also tend to be greater under shrubs than in interspaces (Guo et al., 1998). High temperatures of fires below shrubs kill seeds in the soil, destroying both exotic and native seed banks in the process (Abella et al., 2009; Esque et al., 2010). Although *Bromus* plant density is greatly reduced immediately after fire, over time the abundance of *Bromus* in burned areas often rebounds to exceed pre-burn levels (Brooks, 2002). However, the literature is mixed on the role of fire in accelerating dominance of exotic species. Steers and Allen (2011) concluded that once an exotic species becomes abundant, native species could decline with or without fire.

Burned areas can have notably different ecosystem properties than unburned areas as a result of fire. Not only do fires remove above ground vegetation, but they also alter species composition and affect the structure of mature plant communities, many of which do not recover their former species composition even decades after burning (Engel and Abella, 2011). Fires can also increase soil nutrients, like inorganic soil N that can affect above ground vegetation and increase plant and seed production (Esque et al., 2010; Schneider and Allen, 2012). Broadly, however, in their review of post-fire desert soils, Allen et al. (2011) reported no clear patterns of changes in soil nutrients after fire because changes can be subtle and vary among fires and sites. Some soil nutrients may increase, decrease, or not change after burning (Allen et al., 2011). As a result, it is unclear whether post-fire soil and environmental factors play a role in longevity of *Bromus* seeds.

Since being introduced in the late nineteenth century, *Bromus* has become a dominant annual in many parts of the Mojave Desert (Salo, 2005) where populations grow in dense stands, sometimes exceeding 6000 plants m^{-2} (Salo, 2004). Individual *Bromus* plants are prolific seed producers, generating anywhere from 75 to over 200 seeds per plant (Smith et al., 2000; Wu and Jain, 1979). While *Bromus* may not produce more seeds per plant than natives, its seeds are able to germinate with as little as 2.5 cm of rainfall, considerably less than many native annual species (Beatley, 1966). Earlier timing of germination in the winter coupled with high germination rates provides *Bromus* an advantage over native annuals. This is especially notable in years of high rainfall where the early establishment and prolonged growth of *Bromus* results in greater soil moisture and nutrient uptake, outcompeting native annuals in the process (Salo, 2004).

The longevity of exotic seeds in the seed bank plays an important role in the population dynamics of invaders in native habitats. For example, consecutive years of drought can result in *Bromus* population crashes providing native annuals an opportunity to rebound (Salo, 2004). Instead of maintaining a persistent seed bank that can withstand drought, *Bromus* is thought to rely primarily on the annual production, dispersal, germination of seeds, and emergence of seedlings to maintain populations over time (Salo, 2004). Venable and Brown (1988) describe dispersal and dormancy strategies as inversely correlated in desert annuals, suggesting that since *Bromus* tends toward annual seed dispersal and high germination rates as its strategy, it is less likely that seeds will remain viable in the soil for an extended period of time. Indeed, *Bromus* seeds are generally thought to exhibit little to no dormancy (DeFalco et al., 2003). However, mature seeds do exhibit high-temperature dormancy during months of extreme temperatures and low precipitation, as in the summer months before winter germination (Corbineau et al., 1992). Seeds can also remain dormant in dry storage for several years (Hulbert, 1955).

In years when precipitation is adequate for the emergence and growth of seedlings, the seed bank is thought to decline over time due to near total germination (Salo, 2004). However, this decline may be offset by high seed production of the plants during high rainfall years. Germination rates in *Bromus* have been reported to range from 70% (Corbineau et al., 1992) to nearly 100% (Wu and Jain, 1979). This suggests a transient rather than persistent *Bromus* seed bank. However, Brooks (2000) postulated that some *Bromus* seeds in the soil appear to remain viable for two to three years, but this question has yet to be empirically tested. In a census of dormant seeds in the soil, Wu and Jain (1979) estimated that less than 2% of *Bromus* seeds remain viable for longer than one year. Most information regarding the longevity of *Bromus* seeds in the soil is largely anecdotal, revealing a gap in our understanding of the population dynamics of *Bromus*. Additionally, effects of burial on longevity of viable *Bromus* seeds remain unclear. Research on similar species can suggest hypotheses as to how *Bromus* seeds behave. For example, buried seeds of *Bromus tectorum*, *Bromus hordeaceus*, and *Bromus sterilis* remain viable in smaller proportions than unburied seeds on the soil surface (Jensen, 2009; Meyer et al., 1997; Narwal et al., 2008). Studies also suggest that buried seeds are more likely to germinate than seeds that remain uncovered, as Gleichsner and Appleby (1989) reported for *Bromus rigidus*.

The purpose of this study was to empirically examine longevity of *Bromus* seeds in the soil. We hypothesized that (1) proportions of viable *Bromus* seeds will decrease over time with only a small proportion remaining viable after 24 months; (2) proportions of viable seeds will decrease with greater burial depths; and (3) proportions of viable seeds will differ between seeds collected from burned and unburned areas, although in what way they will differ is harder to predict. Experimental seed enclosures were buried in the field to test effects of time since burial and burial depth on *Bromus* seeds from burned and unburned areas of recent Mojave Desert fire sites.

2. Materials and methods

2.1. Study area

We conducted this study in Red Rock Canyon National Conservation Area (RRCNCA) located in the Mojave Desert, 25 km west of Las Vegas, Nevada, USA. The Mojave Desert is classified as a hot, arid desert with most precipitation falling in the winter months between October and April in the Las Vegas Area (Webb et al., 2009). A weather station at RRCNCA (36°5′ N 115°27′ W, at a middle elevation of 1152 m) has recorded an average of 11.4 cm yr^{-1} of precipitation, a daily low January temperature of −1.6 °C, and a daily high July temperature of 36 °C (1981–2010 records; http://www.wrcc.dri.edu). Several above-average rainfall events occurred during the study, resulting in an above-average annual precipitation (Fig. A1). Average monthly minimum and maximum temperatures were comparable to long-term averages. Seven fire sites were selected with paired burned and unburned plots at each site (Table A1). The fires occurred between 2005 and 2007, two to four years before the beginning of the study, and varied in size between 17 and 13,585 ha burned. Plots ranged from 1030 to 1273 m elevation, which are middle elevations where *Bromus* is most abundant in the Mojave Desert (Brooks, 2009). Fire sites ranged from a distance of 1.5 km to 7.5 km apart.

2.2. Study design

Mature seeds were gathered in late May 2009 from randomly selected plants along a 15 × 2 m transect on both burned and unburned plots at each fire site. Seed collections from each site and burn condition were stored separately in paper bags at room