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Short-term effects of experimental fires on a Mojave Desert seed bank

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ABSTRACT

A Mojave Desert shrub community was experimentally burned to understand changes in seed bank of desert annual plant species in response to wildfire. Seed mortality ranged from 55 to 80%, and fire caused significant losses of native and alien annual seeds. *Schismus arabicus*, *Schismus barbatus*, *Bromus madritensis*, *Bromus tectorum*, *Erodium cicutarium* and *Plantago* spp. made up >95% of the seed bank. *Bromus* spp. and *Plantago* spp. had proportionately greater mortality of seeds than did *Schismus* spp. and *E. cicutarium*. *Schismus* spp. can be lodged into soil cracks thus avoiding lethal temperatures. *E. cicutarium* has a self-drilling mechanism that places the seeds at greater depth in the soil. Greater seed mortality occurred beneath shrub canopies than interspaces for most species (*Plantago*, spp., *Bromus* spp., and *E. cicutarium*), but microsite had little effect on *Schismus* spp. Fire reduced the perennial *Ambrosia dumosa* densities under canopies. Fire reduced the mean number of species found in samples by about one species per plot and no species was extirpated on experimental plots. The relative abundances of common species did not change dramatically as a result of fire or microsite, however; seed densities varied by treatment and affected interpretations of species compositions.

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1. Introduction

During the past 3 decades large wildfires in hot deserts have become increasingly common near large mountain ranges (e.g., Spring Mountains in Clark and Nye Counties of southern Nevada) and at the periphery of hot desert shrub lands in western North America (Humphrey, 1974; McAuliffe, 1995; Brooks and Esque, 2003; Brooks and Matchett, 2006). Desert fires ignite and spread rapidly on fine fuels that accumulate following single or successive years of high precipitation (Beatley, 1966; Rogers and Vint, 1987; Hunter, 1991; Alford, 2001; Brooks, 2002). In the Mojave Desert the non-shrub components of fine fuels frequently consist of invasive annual grasses including *Bromus madritensis* (L.) (Salo, 2002), *Bromus tectorum* L., *Schismus arabicus* Nees, and *Schismus barbatus* (L.) Thell. These grasses are ubiquitous in the Mojave Desert, promoting a positive feedback process known as the grass/fire cycle (D'Antonio and Vitousek, 1992). As a result, alien grasses increase and dominate communities while native perennial species decline due to fires (O'Leary and Minnich, 1981; McLaughlin and Bowers, 1982; Brown and Minnich, 1986; Esque et al., 2004; Brooks and Berry, 2006). Furthermore, the invasive Mediterranean annual grasses can outcompete native species for limited resources (Salo, 2004; DeFalco et al., 2007) and can outnumber native annuals after fires (Brooks, 1999a).

Seed banks represent the current and future potential for plant populations to persist in spite of tremendous climatic variation in hot deserts. Small seeds are most abundant and relatively large seeds produced by many perennial plant species are rare in hot desert seed banks (Guo et al., 2000). Desert plants avoid periods in which there is inadequate moisture to germinate by remaining dormant as seeds during the dry season or years of drought (Kemp, 1989; Baskin and Baskin, 1998). In the Mojave Desert, adequate precipitation promotes two, nearly exclusive, annual plant floras (Juhren et al., 1956; Beatley, 1974), and perennial species have similar differentiation to a slightly lesser extent. Winter annuals germinate at cool temperatures (15–20 °C) and summer annuals germinate at higher temperatures (~25–35 °C; Baskin and Baskin, 1998). This research focuses on winter annuals which are most prevalent in this part of the desert and are most strongly implicated in the grass/fire cycle. In the seed bank, propagules are distributed heterogeneously, thus exposing them to a variety of environmental conditions and ensuring further variability in germination and establishment success (Halvorson and Patten, 1975; Reichman and Oberstein, 1977; Reichman, 1984; Price and Reichman, 1987; Price

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and Joyner, 1997; Guo, 1998). The interspecies variability in optimal conditions for breaking dormancy and subsequent germination and plant growth produce tremendous variability in the plant community composition that is expressed in any single year (Beatley, 1974; Pake and Venable, 1995). Therefore, simply quantifying aboveground production of plants overlooks valuable information available for the study of plant population demography and community composition.

The pattern of fire and plant community impoverishment is established (Brooks, 1999b), but the mechanisms of post-fire seed bank changes are not described for the Mojave Desert. Fires have been shown to reduce annual and perennial plant seed banks in the semi-arid Great Basin (Young and Evans, 1975; Hassan and West, 1986; Billings, 1990; Humphrey and Schupp, 2001), but this relationship has not been quantified in the Mojave Desert. We examined the immediate effects of moderate temperature experimental fires on the seed banks by asking the following questions: 1) How do the densities of native seed banks compare to those of invasive species' seed banks on unburned and burned sites; 2) How does microsite affect the seed banks before and after fire; 3) How does species composition vary in response to fire.

2. Materials and methods

2.1. Study area

The study area was in Parashant National Monument, Mohave County, Arizona (36°25′N, 113°55′W) ranging between 800 and 1000 m above mean sea level. Average annual precipitation between 1957 and 1992 at the nearest NOAA weather station (Littlefield, Arizona, ~50 km to the north) was 208 ± 15 mm (NOAA, 2003), with 60% falling in October through April. The Mojave Desert scrub community is dominated by *Larrea tridentata* (DC) Cov. and *Ambrosia dumosa* (A. Gray) Payne, with *Yucca brevifolia* Engelm. as a conspicuous sub-dominant species (Brown, 1982). Winter and summer annual plant floras overlap little, each responding preferentially to seasonal combinations of precipitation, temperature, and timing (Beatley, 1974). The study site is located on an ancient lava flow with friable soils <300 mm deep at the south end, grading into soils >500 mm deep at the north end of the study area.

2.2. Research design

In a larger companion experiment, sixty 20 m × 20 m plots were established in a random complete block design with six blocks and ten plots per block (Esque, 2004). One-half of plots were treated with fire for the burned treatment and only these plots were used in this experiment. Soil seed bank samples were collected before and after the fire treatments. The plots were established within 100 m of a graded access road and were separated by >80 m. All plots represented the same vegetation association and were located away from anthropogenic disturbances such as abandoned roads and trails.

Each plot was fenced with fine 1-m tall wire mesh (1.25 cm) and surrounded by 20 cm tall flashing to exclude and/or include ants and/or rodents as part of the larger and longer duration companion experiment (Esque, 2004).

2.3. Fuel and fire management

Experimental fires were conducted between 16 and 22 September, 1998. Fine fuels (non-woody) were almost non-existent and insufficient fuels were available to carry a fire across canopy interspaces to mimic Mojave Desert wildfire behavior (Esque, 2004). Therefore, fuels were supplemented using a mixture of Sudan/Bermuda grass (*Sorghum sudanense* (L.) Pers. and *Cynodon dactylon* (L.) Pers.). We conducted several small (4 m^2–8 m^2) test fires and one larger one (400 m^2), which included burning desert shrubs, to determine the correct amount of fuel required to mimic the intensity of desert fires we observed prior to this occasion. Hay was spread 30 min prior to ignition and was applied by hand at 127 kg/0.04 ha treatment plot (3175 kg/ha), which is near the upper limit for aboveground spring annual plant production in the region (*unpublished data*). Supplemental fuels were placed among shrubs and evenly in interspaces to mimic fuel loads observed during wildfires. Fires were ignited with a portable propane torch on the upwind side of the plot and set in a continuous line so that the fire was carried by the wind and simulated desert wildfires. Once ignited, fires burned steadily across each study plot leaving behind a layer of blackened ash. Mean peak temperatures (±SE) were measured in real time and ranged from 399 ± 88 °C in interspaces ($N = 40$) to 579 ± 133 °C in *Ambrosia* (Esque, 2004). The fire moved steadily across the plots and residence times were mostly less than 5 min for elevated temperatures. However, the fire had some heterogeneity and the bases of shrubs burned the longest. Small amounts of unburned hay were removed from the plots immediately after burning, and additional unburned and burned fuels were also gathered as they collected against bordering wire mesh fences.

2.4. Collection of seed bank samples

Unburned samples were collected in 14 August 1998 and burned samples were collected on 13–15 October 1998. We assumed for this experiment that the season of work, the low spring annual production, the short lead-time from fence establishment to treatments, and the relatively short (2 month) time span between sampling the seed bank before and sampling after burning were largely insufficient for ants and rodents to affect the seed bank in this experiment. Within each 20 m × 20 m plot, soil samples were collected in three randomly selected canopy (*Larrea* or *Ambrosia*), and three interspace microsites. Species of the plant providing the canopy microsite were not addressed because the distribution of seeds is typically influenced more by microtopography than shrub species (Price and Reichman, 1987). Samples within canopy microsites were collected between the stems and the outermost vegetative parts of canopies; interspace samples were collected more than 1 m outside the canopies of perennial plants. Within each microsite, four soil samples were collected at the cardinal directions and pooled. Separate shrubs were used to sample pre- and post-fire canopy microsites.

Soil samples were collected using soil tins to a depth of 3 cm (diameter 6 cm), because the majority of seeds in the seed bank occur close to the soil surface (Young et al., 1975; Nelson and Chew, 1977; Ferrandis et al., 2001). Each individual sample contained 85 cm^3 of soil. All four soil samples within a microsite were pooled (85 $cm^3 \times 4 = 340$ cm^3) and then all samples from either the shrub canopy or interspace microsites were pooled such that there was one sample for each microsite type for each study plot which was the experimental unit (340 $cm^3 \times 3$ canopy microsites = 1020 cm^3).

2.5. Seed bank assay

Methods of assaying seed banks were first developed in the past century to quantify agricultural weed infestations among crops (Brenchley and Warington, 1930) and later generalized for other habitat types (Mayer and Poljakoff-Mayber, 1982). Variations on seed bank assay methods have been used often (Juhren et al., 1956; Coffin and Lauenroth, 1990; Odgers, 1994). Seed bank assays use the density of seedlings that emerge from treated soil samples as

a proxy for soil seed density, and results refer to the enumeration of "seeds". We use the term "seed" as a generalized term in reference to a variety of plant propagules including the naked caryopsis of *Schismus* spp. and the fruit of *Erodium cicutarium*. We modified seed bank assay methods that were developed for research projects at sites in the Great Basin of western North America (Young et al., 1969; Young and Evans, 1975; and Young et al., 1981).

Soil seed bank samples were mixed thoroughly, soil aggregates were crushed, and litter and rocks >1 cm diameter were removed. A volume of 120 cm^3 was used for each germination trial for a rough estimate of 40 cm^2 of surface area (3 cm deep). Each cleaned and pooled soil sample was placed in a plastic pot (15.3 cm diameter × 6.8 cm tall) lined with a large unbleached coffee filter, and 120 cm^3 of vermiculite were added on top of each soil sample to maintain moisture. When spread across the bottom of each pot the soil samples were 1.5 cm deep and were covered by a similar depth of vermiculite. Some seeds are sensitive to the amount of incidental light available for their germination (Gutterman, 2002). Vermiculate did not completely cover the soil surface after initial watering and thus seeds on the surface of the soil layer had some exposure to light. Furthermore, subsequent to each drying period and prior to re-wetting the soils the soil samples were thoroughly mixed to provide variation in surface exposure to the seeds in the samples. All of the pots were arranged randomly on benches in a greenhouse.

The seed bank assay samples were subjected to four separate greenhouse treatments, consecutively, with periods to dry out completely between each treatment. Each pot represents either a canopy or interspace microsite within one of the study plots. Since there were 60 study plots and two microsites per study plot, the result is 120 experimental units. Treatments included two wetting phases with tap water, a third wetting phase with 50 mL of a 0.01 M solution of potassium nitrate (Mayer and Poljakoff-Mayber, 1982) and a fourth wetting phase with 50 mL of a 6.5×10^{-4} M solution of gibberellic acid (Young et al., 1969). Moisture content and timing can be important to the germination of desert plant species (Adondakis and Venable, 2004). Moisture content of the soil samples was monitored daily and the pots were kept moist by watering the pots every-other-day. Pots were watered to the extent that water drained from the bottoms of the pots, yet because the soils drained very well due to bench construction, no standing water remained in pots (DeFalco et al., 2009). Samples were air dried between each treatment to simulate the annual dry seasons required for some species to germinate. The pots were dried for 3–4 weeks, before starting the next wetting phase.

2.6. Cotyledon identification

Vouchers were collected of each plant species that emerged from the pots. Some of the plants that could not be identified at the cotyledon stage were moved into pots to grow into adult plants for identification. Additional soil samples from the study area were germinated in larger pots to facilitate identification. Some of the seedlings could not be identified, so they were lumped by genus. The most prevalent of these, *B. madritensis* ssp. *rubens* and *B. tectorum* are hereafter referred to as *Bromus*; *S. arabicus* and *S. barbatus* are referred to as *Schismus*; and *Plantago patagonica* and possibly others are referred to only as *Plantago*. *Schismus* could not readily be differentiated from *Vulpia octoflora* which was very rare in the samples that were grown for identification, and were lumped in the results of this experiment. Ancillary samples of soils that were germinated to maturity in large pots indicated that *Vulpia* was always rare during this experiment, and this pattern was corroborated by samples of vegetation cover (Esque, 2004). After initial use of a species name, plants represented by a single species are referred to by genus only, unless a new species is used.

2.7. Statistical analyses

Seed density (number of individual seeds/0.01 m^2) and number of species per sample were analyzed in split plot factorial analyses of variance (ANOVA). Although often referred to as species richness, this study involved such a small surface area that we refer simply to number of species per sample. Fire (pre- versus post-) was used as a full plot effect, and microsite (interspace versus canopy) was analyzed as a sub-unit within each plot (Littel et al., 1996). The seed banks of annual and herbaceous perennial plants were analyzed separately from woody perennial and succulent seeds. A MANOVA was conducted to analyze the variation in seed bank densities contributed by all species collectively. Separate ANOVA analyses were used to examine individual species to understand the nature of the significant interaction in the MANOVA. The multiple ANOVA analyses for individual species were corrected using Bonferroni's inequality with α set at $P < 0.0125$ to correct for the use of multiple ANOVA analyses (Quinn and Keough, 2002). Providing direct comparisons of species richness in response to treatments can be particularly misleading if the treatments applied cause great variation in number of individuals involved (Peet, 1975). The relationships between seed densities and species richness among fire treatments and microsites were analyzed by rarefaction analyses (Gotelli and Colwell, 2001) using the EstimateS program (Colwell, 2005).

3. Results

Prior to fire, total seed densities under canopies were greater than interspaces ($F_{1,\ 111} = 3.5$; $P = 0.06$; Fig. 1); and, there were proportionately greater losses of seeds under the shrub canopies as a result of burning those sites ($F_{1,\ 111} = 17.2$; $P < 0.01$). There was an order of magnitude more alien seeds than native seeds, both before and after the sites were burned (Fig. 2). Native and alien annual species each had significant decreases of seed densities as a result of fire ($F_{1,\ 95} = 5.4$; $P = 0.03$ and $F_{1,\ 111} = 28.4$; $P < 0.01$, respectively), and aliens lost proportionately more seed than natives (Fig. 2). Although, on average, there were higher densities of alien plant seeds under canopies than interspaces prior to fire (300 ± 50.5 versus 245.1 ± 67.5, $N = 30$ respectively), more alien seeds were lost under shrub canopies (fire × microsite, $F_{1,\ 95} = 3.44$; $P = 0.06$).

Four of the 24 species identified in germination assays were abundant enough to include in the MANOVA. The combined average densities of the *Schismus*, *Bromus*, *Erodium* and *Plantago*

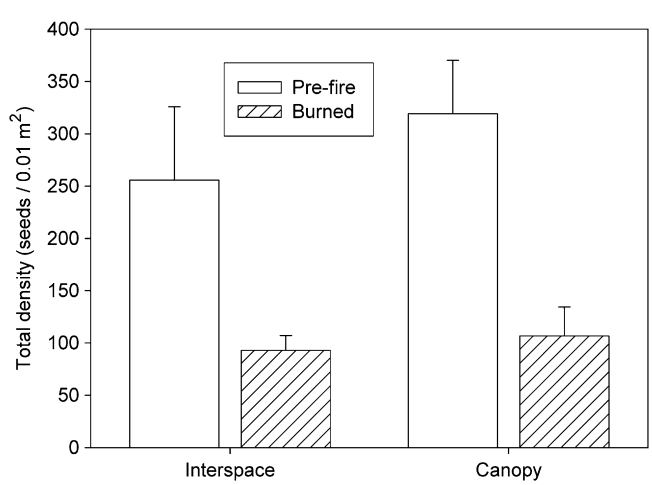

Fig. 1. Total seed densities (mean ± 1SE, $N = 120$) beneath shrub canopies and in interspaces before and after experimental fires at Parashant National Monument, Arizona in October 1998.

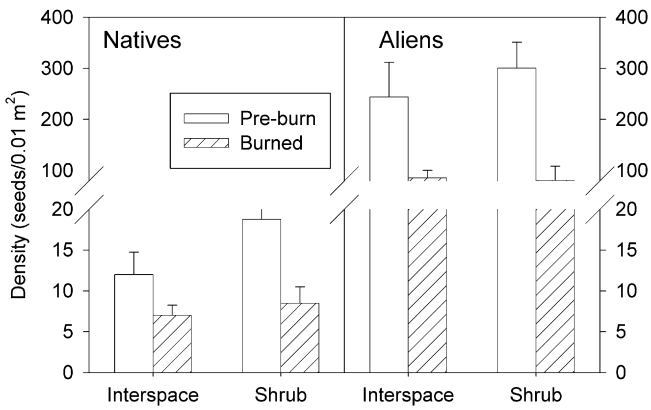

Fig. 2. Fire effects on total native and alien seed densities (mean ± 1SE, $N = 120$) in interspaces and shrub canopies at Parashant National Monument, Arizona in October 1998.

seeds made up >95% of the seeds on all sites that were burned. *Schismus* significantly outnumbered all other seed categories (90% of seed bank averaged across all treatments), with 66% of the seeds in unburned-canopy sites and greater than 88% in all other treatment combinations.

Fire reduced *Schismus* seed densities similarly between microsites (Table 1) and seed densities were not different between interspaces and beneath canopies (Table 1). *Bromus*, the second most abundant species (28% of seed categories combined), and the less abundant species *Erodium* both declined to a greater extent beneath canopies than in interspaces (fire × microsite, Table 2). *Plantago* were the only native species among the common seed types and ranged between 2 and 4% of total seeds in all treatment categories. *Plantago* seed densities were not different among microsites (Table 1), but burning caused a significant decline in seed density. The 59% loss of *Plantago* due to fire was moderate compared with the other species in this experiment. *Erodium* was the least abundant of the common species ranging from less than 1–3% of the total seed densities in any treatment combination.

3.1. Plant community composition and species richness

Of the 24 species differentiated using seedling germination, 8 were common to all treatment combinations, and these included species with greater than 1% of the total seed density (*i.e., Schismus*, *Bromus*, *Plantago*, *Ambrosia*, *Erodium*, *Pectocarya recurvata*, *Draba cuneifolia*, *Descurainia pinnata*, and *Eriophyllum lanosum*). Another eight species were found only among unburned plots, and five were found only on burned plots, all of which were uncommon and not identified to species. One species, *Bouteloua aristidoides* was unique to interspaces. The mean species richness was not different among microsites ($F_{1,111} = 2.2$; $P = 0.14$; Fig. 3A), but when the interaction between fire and microsite was considered, burned-canopy microsites had fewer species than unburned- canopies (11.6 ± 0.5 versus 7.7 ± 0.7 species, $N = 30$) and interspaces had a proportionately smaller but significant change in species between burned and unburned sites (fire × microsite; $F_{1,111} = 4.7$; $P = 0.03$; Fig. 3A). Using rarefaction analysis unburned canopy also had the highest species richness (95% CI = 15.7–30.3 species) yet was indistinguishable from the other treatments as seen through the overlapping confidence intervals: burned canopy (12.1–23.9), burned interspace (9.3–20.7), and unburned interspace (8.4–19.6; Fig. 3B). Furthermore, the rarefaction curves did not reach their asymptotes and this was more pronounced for the burned sites where seed densities were lower

Table 1
Seed densities (# of seeds/0.01 m^2) for annual plant species with respect to fire (unburn or burn) and microsite (shrub canopy or interspace) in the Pakoon Basin of Grand Canyon/Parashant National Monument, the Pakoon Basin of Grand Canyon/Parashant National Monument, 1998.

Species	Unburn		Burn	
	Interspace	Shrub Canopy	Interspace	Shrub Canopy
	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Pectorcarya recurvata	0.2 (0.14)	0.8 (0.25)	0.1 (0.08)	0.5 (0.31)
Eriophyllum lanosum	0.8 (0.18)	0.5 (0.24)	0.8 (0.26)	0.3 (0.14)
Erodium cicutarium	1.1 (0.40)	2.0 (0.35)	0.9 (0.29)	0.8 (0.22)
Plantago patagonica	3.6 (0.82)	3.0 (0.88)	1.3 (0.28)	1.4 (0.57)
Bromus spp.	4.2 (1.00)	35.1 (5.17)	1.0 (0.23)	1.3 (0.36)
Schismus spp.	92.1 (27.24)	83.4 (17.96)	32.4 (0.08)	37.2 (10.98)

Table 2
Statistical results of separate univariate ANOVAs with fire and microsite as main factors and density of seed species as response factors (DF 1106 for all analyses, $N = 120$).

Species	Source	F	*P*-value
Schismus spp.	Fire	8.30	<0.01
	Microsite	1.04	0.31
	Fire × Microsite	0.98	0.33
Bromus spp.	Fire	141.79	<0.01
	Microsite	67.86	<0.01
	Fire × Microsite	64.73	<0.01
Plantago spp.	Fire	8.52	<0.01
	Microsite	2.35	0.13
	Fire × Microsite	0.06	0.80
Erodium cicutarium	Fire	6.55	0.01
	Microsite	4.88	0.03
	Fire × Microsite	6.33	0.01

3.1.1. Perennial plant seeds

Four woody or succulent perennial plant species were identified using the seedling germination method including *Ambrosia*, *Gutierrezia sarothrae*, *Larrea*, and *Cylindropuntia acanthocarpa*. These species occurred in less than 25% of germination samples. Perennials were so rare in the seed bank that statistical analysis was not possible. Burning had little effect on the abundance of *Ambrosia* seed in interspaces, but reduced the seed densities under canopies so that they were about equivalent to interspace densities (i.e., 0.25 ± 0.18 ind/0.01 m^2). Seed densities of *Ambrosia* declined (Fig. 4), but post-fire plots had a greater density of *Gutierrezia* after fire (0.08 ± 0.08 on unburned to 0.33 ± 0.26 ind/0.01 m^2 on burned), as did *Larrea* (0–0.17 ± 0.17). *Gutierrezia* seeds were found in samples for two burned plots versus one unburned plot, and the differences were even smaller for *Larrea*. *Opuntia* were not identified on any plots in 1998. The values for some of these perennial species were so low that the observations could be due to chance variation.

4. Discussion

The amount and arrangement of the fuel we used was sufficient to mimic desert wildfires frequently fought in the Pakoon Basin during the past decade (L. Evers, *personal communication* – US Forest Service). Although geometry of fuels resulting from desert annual vegetation would be extremely difficult to mimic (requiring thousands of vertical stems per m^2 of habitat), we arranged fuels above ground so that the end result was a fire with flame lengths of 1 m–3 m and residence times of a few seconds to several minutes (Esque, 2004). Quantitatively, the intensity of this fire was similar to ground fires quantified during experiments in ponderosa pine savannahs that burned as a result of *B. tectorum* as part of the fuels

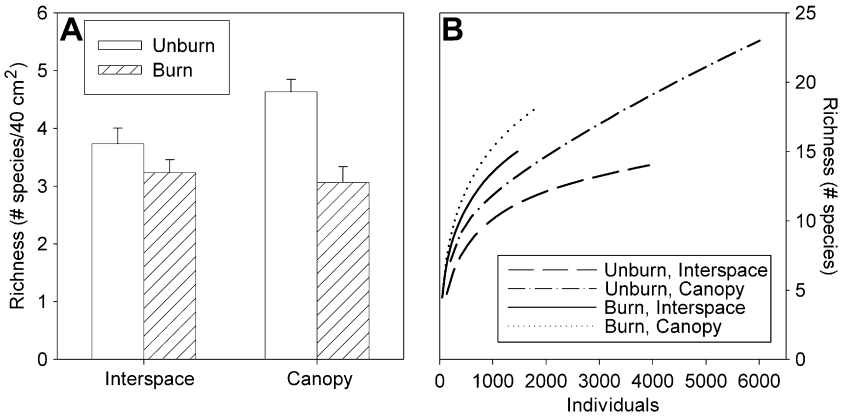

Fig. 3. A) Comparison of the effects of fire and microsite on species richness (number of species/0.01 m^2) in samples at Parashant National Monument, Arizona in October 1998. B) Rarefaction curves relating species richness to the number of samples collected.

(Keeley and McGinnis, 2007); however, temperatures for other wildfires in Mojave Desert shrub habitats have not been quantified for comparison.

Peak temperatures of 100–225 °C were sufficient to kill seeds in the soil (*citations in* Baskin and Baskin, 1998; Esque, 2004) and near the maximum expected for this vegetation type based on the fuel load used in this study (Brooks, 2002; Esque, 2004). As a result, seed losses ranged from 55 to 80% and were similar among species and microsites with one exception: seed mortality was higher in canopy microsites for *Bromus* (96%). In another study, large losses of *Bromus* spp. after fire resulted in declines in total above ground plant production on those sites, while *Erodium* production was unaffected (Brooks, 2002). *Bromus* suffered proportionally large seed losses in canopies where it was most abundant prior to burning. *B. tectorum*, an alien annual species linked to plant community changes in the Great Basin, had comparable seed losses of 80–96% immediately after fires (Young et al., 1976; Hassan and West, 1986; Humphrey and Schupp, 2001). In the Great Basin, seeds of *B. tectorum* normally accumulate in the deep canopy litter, and significant losses occur in this microsite where fires are hottest compared to interspaces (Young et al., 1976). Quantification of seedlings *in situ* indicates that shrub canopies have diminished seed reserves after fires in the Mojave Desert (Brooks, 2002).

In contrast to *Bromus*, proportionally more seeds of *Schismus* and *Erodium* appear to have survived by avoiding lethal temperatures, each by a different means. *Schismus* spp. have miniscule caryopses (Gutterman, 1994), and *S. arabicus* have been documented to slip into minute soil surface fractures thus avoiding predation (Gutterman, 1994) and erosion by wind and water (Boeken and Shachak, 1994). This characteristic first described as predator and dispersal avoidance also appears to provide a means for this species to avoid lethal temperatures. The insulative property of mineral soil just below the soil surface has the potential to provide seeds a survival advantage. If seeds occupy a position in the soil that is greater than 1 cm deep, then they have a significant advantage over the same seed species at shallower depths because the temperature in mineral soils is dramatically reduced with depth (Esque, 2004).

Alternatively, species of *Erodium* have a highly modified carpel with a moisture activated hygroscopic awn (Young et al., 1975; Stamp, 1984) providing the seeds a mechanism to drill the carpel to greater soil depths. This action may provide a way to: 1) increase seed to soil contact for germination; 2) avoid being collected and eaten by seed predators; and 3) avoid lethal temperatures during fires. Based on empirically measured soil temperatures during experimental fires, seeds that are capable of self-drilling at least 1 cm into mineral soils have a much greater chance of escaping lethal temperatures during high intensity fires (Esque, 2004). *Erodium* are adapted to colonize bare soils and are less abundant in continuous grass litter (Young et al., 1975). Litter may prevent the self-drilling seeds from penetrating into the mineral soil and explain the higher mortality of *Erodium* spp. seeds beneath shrubs. In combination with the lower temperatures expected in interspace microsites during fires (Patten and Cave, 1984), *E. cicutarium* has characteristics that provide a survival advantage over other abundant species during fire while also avoiding predation and increasing chances for germination.

Seed of *Schismus* spp. can reach prodigious numbers in the Mojave and Sonoran deserts of North America, even in the absence of fire. Halvorson and Patten (1975) included *Schismus* spp. among the most numerous species expressed in terms of plant density in the Arizona Upland of the Sonoran Desert in association with fire. On the basis of biomass, *Schismus* spp. was the most abundant species in 1994 and 1996 in the western Mojave Desert (Brooks, 1999b). *Schismus* spp. was the most abundant seed species in the seed rain and ranked fifth among the 21 most abundant species identified in the seed bank in the central Mojave Desert (Price and Joyner, 1997). Based on the responses of older burned sites in the Pakoon Basin of northwest Arizona, we expected to see more *B. madritensis* in response to fire. The dominance of *Bromus* spp. versus *Schismus* spp. may vary depending on climate conditions and other factors. Seed bank results reported here were consistent with all of the previous

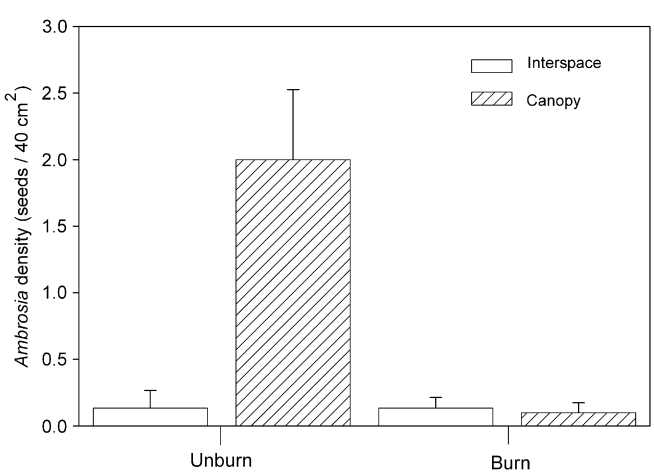

Fig. 4. Comparison of the effects of fire and microsite on *Ambrosia dumosa* at Parashant National Monument, Arizona in October 1998.

data indicating that the alien *Schismus* may be the most numerous species in low elevation Mojave Desert shrub lands.

On average, the numbers of species found in soil samples were reduced by about one species per plot by fires. Consistent results were found for an experiment that examined plant community change by quantifying aboveground plant production in the western Mojave Desert (Brooks, 2002). The average loss of only one species highlights consistency of the pattern; however, it should be noted that the smaller sample area of the experimental plots in this study (0.01 m^2) might not be comparable for identifying differences in actual species richness with other studies, because species richness is area dependent (MacArthur and Wilson, 1967). Small sample areas resulted in fewer than 10 annual plant species (natives and aliens combined) per experimental plot. The reduction in the number of species indicates that the species can no longer be detected in the sample. However, the species probably still exist in the landscape at extremely low levels, but the sampling design used here cannot discern a tendency toward extirpation from those that are merely rare. This is partially explained by the rarefaction analyses, which illustrate that species richness values had not yet maximized for burned or unburned sites within canopies or interspaces.

Factors that may have affected the variability in the responses to treatments, other than environmental conditions and seed biology include the seed germination techniques. Seed germination techniques are logistically intense, and rarefaction analyses indicated that we had not entirely saturated species richness with the sampling intensity that was possible during this experiment. Even if sampling were not limiting, the germination of each species depends on the appropriate amount and timing of moisture, temperature and light (Gutterman, 2002) and it is unlikely that experiments will ever completely expend the seed germination potential of soil samples. However, this technique continues to provide useful insights into seed bank variation and composition and continued will likely improve these techniques.

Although some species of desert annuals with moderate densities had large losses of seeds following fire (e.g., native *Plantago*), no single species was consistently eliminated on all plots. Seed damage depends on the duration and intensity of temperature exposure, which can be affected by seed characteristics (Wright, 1931; McKell et al., 1962) and seed juxtaposition in the microsite. Therefore, the mortality of seeds due to high fire temperatures and exposure duration varies by species and environmental conditions. More studies about the physical characteristics of desert seeds that influence their survival during fires are required to understand these patterns (Fotheringham, 1999).

Perennial plant seeds were very rare in all of the samples we collected. We conclude that the most likely reason for the minor increases we observed in the seeds of *Gutierrezia* and *Larrea* after fire were due to error related to small sampling size. However, the experiments we conducted were not designed to consider the effect of serotiny, which could have resulted in greater germination after exposure to fire or associated smoke (Fotheringham, 2009). Alternatively, the seeds of these species may have found their way into the plots However, due to other aspects of the research, the plots where the seeds originated were surrounded by 1 m tall mesh fencing to omit rodents and flashing to omit ants, thus wind transport was also highly unlikely for these plots. When studies of changes in perennial plant seed banks in the Mojave Desert is of particular interest, then alternative methods incorporating larger soil samples are required to reduce variability due to samples with zero seeds (e.g. methods in DeFalco et al., 2009).

Seed bank experiments are used to understand the patterns observed in the post-fire desert environment because they provide a more direct view of the restoration status of burned areas than simply sampling the above ground vegetation. This information can be used to direct experiments and management actions designed for restoration of disturbed areas.

Disproportionate seed mortality among species can stem from a variety of environmental conditions and seed characteristics including seed abundance, variability in temperatures, seed size and both passive and active temperature avoidance (Baskin and Baskin, 1998). *Schismus* seeds, which are among the smallest and would be among the most vulnerable simply in terms of heat physics, apparently have a means to avoid lethal temperatures over many other seed types. While in one of their places of origin – the Negev Desert of Israel – *Schismus* are viewed as having passive predator avoidance, but the same mechanism appears to provide an advantage over fire where they have naturalized in North America. Alternatively, *Erodium* seeds actively avoid thermal extremes by means of physical movements deeper into the soil profile. In contrast, *Bromus* spp. apparently have no such means to increase their survival, yet can be quite abundant in the post-fire environment under certain conditions (Young et al., 1976; Esque et al., 2004). Other seeds may benefit from similar passive or active heat avoidance, but numbers were insufficient to detect such a pattern and further work involving seed bank survival and fires would be useful to understand these patterns.

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