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# SEED BANKS OF *BROMUS TECTORUM*–DOMINATED COMMUNITIES IN THE GREAT BASIN

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ABSTRACT.—Many shrub-steppe communities of the Great Basin have been converted to *Bromus tectorum*–dominated communities. Seed production and seed bank traits of native perennials may be poorly suited to conditions of communities dominated by this introduced annual, and native perennials may be lost from the seed banks. Seed banks of former shrub-steppe communities now dominated by annuals were quantified on 3 sites in western Utah to determine if seeds of native perennials were present and to track changes in *Bromus tectorum* seed densities and species composition of seed banks after fire. Burned and unburned plots on 1 site were sampled for 3 years after a wildfire. Plots consisted of grids of 5.2-cm-diameter soil cores. Seeds were quantified by monitoring seedling emergence from these cores over an extended period of time in the greenhouse. On unburned plots introduced annuals, mainly *Bromus tectorum*, constituted >99% of the seed bank, with *Bromus* densities of 4800–12,800 seeds $m^{-2}$. Immediately after the fire, *Bromus* seed density was <3% of unburned plots, but its seed bank density recovered in 2 years. The major change in species composition of the seed bank following fire was a shift in proportional abundance between *Bromus* and 2 other introduced annuals immediately after the fire. One native annual and a native annual/perennial (*Oenothera pallida*) increased in the seed bank the 1st year after the fire. Of all samples, only 4 perennial-plant seeds representing 3 species (excluding *Oenothera)* were found, for a total perennial-plant seed bank of 2–3 seeds $m^{-2}$. Lack of perennial-plant seeds in annual-dominated communities impairs the reestablishment of native perennials. Because perennial-plant seeds are so few, the reduction of *Bromus* seed banks by fire provides no opportunity for reestablishment of native species.

*Key words: seed bank,* Bromus tectorum, *Great Basin, shrub-steppe, seed dormancy, annuals, perennials.*

Unlike warm-desert plant communities, native Great Basin shrub-steppe plant communities usually have a low diversity of annuals (Kemp 1989). Perennial-plant seeds are a greater component of the seed bank, and total seed densities are lower overall than in warm deserts (e.g., Hassan and West 1986). When annuals are a major component of plant communities in the Great Basin, they are usually spring-growing introduced Eurasian species. These invaded Great Basin plant communities have seed bank characteristics more like those of warm deserts, with annual-plant seeds as a major component of the seed bank, greater overall seed densities, and greater temporal variability of the seed bank (Kemp 1989).

Currently, otherwise similar semiarid Great Basin sites can support either communities dominated by native shrubs and bunchgrasses or communities dominated by the introduced annual grass *Bromus tectorum* (Young and Evans 1973, Pellant 1990). The seed bank of a site is the storage of viable seeds in litter or soil. Individual species can be characterized as producing either a persistent seed bank in which seeds persist in the habitat in a viable condition for longer than 1 year, or a transient seed bank in which none of the seeds persist in the habitat in a viable condition for more than 1 year (Thompson and Grime 1979). Seed longevity is generally less important to persistence of the species on the site for perennials than for annuals in deserts (Noy-Meir 1973, Kemp 1989) and in grasslands (Major and Pyott 1966, Rice 1989). Consistent with this, some important native shrubs and perennial grasses of semiarid Great Basin communities (*Artemisia tridentata,* Young and Evans 1989; *Chrysothamnus nauseosus,* Meyer and McArthur 1987; *Leymus cinereus*, Meyer et al. 1995; and *Pseudoroegneria spicata,* Kitchen and Monsen 1994, Humphrey and Schupp 2001) form no persistent seed bank. However, others (*Achnatherum hymenoides*, Jones 1990; *Sporobolus cryptandrus,* Lippert and Hopkins 1950; most species of *Stipa,* Young 1988; *Atriplex canescens,* Meyer et al. 1987; and *A. confertifolia,* Meyer et al. 1998) do form persistent seed banks. Species with transient seed banks can be completely extirpated from local areas if disturbances

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remove seed-bearing individuals (O'Connor 1991). Native perennials have been greatly depleted on sites in the Great Basin now dominated by *Bromus tectorum* (hereafter referred to as *Bromus*) through a combination of past overgrazing and wildfires. Wildfires occur much more frequently in *Bromus*-dominated communities than in native shrub-steppe communities (Whisenant 1990). Some perennials that resprout after fire may remain in annual-dominated communities. However, because *Bromus* dries and is prone to burn before these perennials set seed, fires frequently prevent them from producing seeds. Although some native perennial species appear to have effective seed dispersal mechanisms, dispersal onto sites where the species do not occur is apparently very limited (Marlette and Anderson 1986). With seed input thus curtailed, perennial-plant seeds may become very rare in annual-dominated communities, contributing to the inability of native perennials to reestablish (West 1983). This would be true especially of species with only a transient seed bank.

Although most *Bromus* seeds are destroyed by wildfires, high seed production from the proportion that remains can quickly replenish the seed bank (Young and Evans 1978, Hassan and West 1986). Most seeds of *Bromus* germinate soon after they are released (autumn–spring after release in summer), but often some are exposed to environmental conditions that cause them to become physiologically dormant (induced dormancy; Young and Evans 1975, Kelrick 1991, Pyke and Novak 1994). Seeds with no dormancy mechanisms can also remain viable in the soil for more than 1 year if they do not encounter conditions that allow germination (Young et al. 1969). Thus, *Bromus* can persist in the seed bank through years when seed input is lacking.

Seed banks of sagebrush-steppe communities (Goodall et al. 1972, Parmenter and MacMahon 1983, Hassan and West 1986) and transitional annual-perennial communities (Young and Evans 1975) have been described, but seed banks of Great Basin communities dominated by introduced annuals have not been described. We quantified soil seed banks of 3 *Bromus*-dominated communities in western Utah. Sampling was timed to include all the transient seed bank (produced in summer and autumn), as well as any persistent seed bank. We asked the following questions: (1) Are seed banks of native perennials present in these annual-dominated communities? (2) How much are *Bromus* seed numbers reduced by fire, and how quickly do they recover? (3) What changes in species composition of the seed bank occur after fire? Our main experiment followed seed bank dynamics on burned and unburned plots for 3 years after a wildfire. We augmented information from this experiment with seed bank data for 1 year from 2 other nearby sites.

## METHODS

All 3 sites are at the U.S. Army Dugway Proving Ground, Tooele County, Utah, USA. The Long-Term site, where seed banks available for the 1996, 1997, and 1998 growing seasons were described, is in a nearly level area below the southeastern foothills of the Cedar Mountains at 1480 m elevation (40°14′30″N, 112°50′10″W). The other 2 sites, where seed banks available for growth only in 1996 were sampled, are a nearly level site 0.5 km from the Long-Term site and at the same elevation, and a gently sloping higher-elevation site (1620 m) at the southeastern end of the Cedar Mountains about 5 km northeast of the Long-Term site (40°16′00″N, 112°49′40″W). All 3 sites have deep (>1 m) sand to loamy fine sand soils (Humphrey and Schupp 1999). Mean annual precipitation for the nearest weather station, about 8 km southwest of the Long-Term site in an open flat, is 20 cm (U.S. Army Dugway Proving Ground, Meteorological Operations Office), but our sites are in a topographic position that is likely to receive more precipitation than this. During the study all 3 sites were dominated by *Bromus* with 2 other introduced annual species common, *Sisymbrium altissimum* and *Salsola iberica.* Native perennial species were almost completely absent from the sites, but a few were present 100–200 m away. Native vegetation was probably transitional between sagebrush-steppe and salt-desert shrub communities. Major native species remaining on surrounding areas with similar soils and topography were *Artemisia tridentata, Sarcobatus vermiculatus, Atriplex canescens, Ephedra nevadensis, Achnatherum hymenoides, Stipa comata,* and *Pleuraphis jamesii*.

At the Long-Term site, burned and unburned plots were paired about 20 m apart on opposite sides of a dirt road that stopped a wildfire in late summer 1995. There were 2 replicates of these burned-unburned pairs. The seed bank on burned and unburned plots was sampled (1) after the wildfire and before any plant growth, (2) after the 1st growing season following the fire, and (3) after the 2nd growing season following the fire (March 1996, March 1997, and February 1998, respectively). At the higher-elevation site, termed the Hill site, 2 replicate burned and unburned plots were located on opposite sides of the border where firefighters had extinguished a wildfire in July 1994. After 1 growing season all plots on this site were burned by another wildfire (the late-summer 1995 fire that burned the Long-Term site). Thus, for the March 1996 sampling time, the 2 treatments represented the seed bank (1) immediately after 1 fire, and (2) immediately after the 2nd of 2 fires that occurred in consecutive years. The site near the Long-Term site, referred to as the Near-Dune site, was only lightly burned by the 1995 fire, with *Bromus* stubble and seeds on the soil surface remaining. On this site only 2 plots, considered to be 2 replicates of a single burn condition, were sampled.

On each site a plot consisted of a grid of 5.2-cm-diameter (21.2 $cm^2$ surface area) soil cores taken to a depth of 4 cm with a steel cylinder. On the Long-Term site in 1996, plots consisted of 30 core samples in a 6 × 5 grid with 2.5-m spacings between samples. Because it was apparent from the 1996 data that seeds of perennial species were extremely rare, we increased numbers of core samples to 40 per plot in an 8 × 5 grid with 2 × 2.5-m spacing between samples in 1997 and 1998 to increase the likelihood of finding perennial-plant seeds. (About 36 cores per plot were used in 1997 because some were later damaged.) At the Hill site each plot consisted of 25 cores taken in a 5 × 5 grid with 6-m spacing between samples. At the Near-Dune site, 24 cores per plot were collected in a 6 × 4 grid with 6 × 3-m spacing between samples. We designed the areas occupied by the grids of samples on these 2 sites to characterize the seed banks of plots used in a revegetation experiment, and thus they were larger than plots at the Long-Term site. These differences in plot sizes should not affect the estimates of seed banks. However, greater numbers of core samples could increase precision of estimates and likelihood of encountering rare species. As a grid of core samples, each plot was intended to give a representation of the seed bank for that treatment that takes into account heterogeneity of the seed bank. Our experimental design was not, however, intended to quantify within-plot heterogeneity.

Similarly, timing of sampling was not intended to address seasonal variation in the seed bank. Instead, we took soil core samples once each year in winter (mid-March 1996, all sites; 8 March 1997 and 19 February 1998, Long-Term site) to quantify the total yearly seed bank, which consisted of seeds produced in summer through autumn plus any persistent seed bank. Taking samples at this time also allowed cold-stratification of seeds to occur in the field. Seeds were quantified by monitoring emergence in the greenhouse. Quantifying germination after cold-stratification has been described as a preferred method for identifying species present in seed banks (Gross 1979). However, species with dormancy that is difficult to break may be underestimated. After identifying and counting field-emerged seedlings, we spread each soil core, along with its associated surface litter, over a base of sand in a 14-cm-diameter pot with the soil core sample forming a layer about 1 cm thick. Pots were placed in a heated greenhouse and watered as needed (every 2–4 days). Seedlings emerging through spring were identified and counted. In addition, we left the pots dry during summer and monitored emergence again through autumn to identify previously dormant autumn-germinating seeds. For the samples from all 3 sites in 1996, greenhouse emergence was censused on 9 April, 8 June, and 22 December 1996. For the 2nd- and 3rd-year samples from the Long-Term site, emergence was censused on 10–11 May, 20 June, and 10 December 1997; and 13 April, 5 May, and 19 December 1998. The quantified soil seed bank consisted of all seedlings that either existed in the core samples at the time they were taken or emerged in the greenhouse. Seed density per plot for each species was the total number of seeds of that species in all cores of the plot divided by the total area of all cores of the plot. Inasmuch as number of cores per plot differed between years and sites, we standardized density estimates to seeds $m^{-2}$.

## RESULTS

As expected, *Bromus* strongly dominated the seed bank on all plots. Although much less abundant than seeds of *Bromus,* seeds of 2 other annuals, *Sisymbrium altissimum* and *Salsola iberica,* greatly outnumbered seeds of any other species overall (Tables 1, 2). Only on the burned plots of the Long-Term site after the 1st growing season following the fire (1997 sampling) was the abundance of any native species in the seed bank greater than 10 seeds $m^{-2}$ (Table 1). These species were an annual, *Mentzelia albicaulis*, and an annual to short-lived perennial, *Oenothera pallida.* Although not previously observed on the plots, these 2 species formed a substantial part of the vegetation in the 1st growing season following the fire on burned plots of the Long-Term site. It was apparently seeds from these plants that appeared in the 1997 seed bank. Despite the increased availability of seeds for 1997, these species were not prominent in 1997 vegetation and their seeds were not found in the 1998 seed bank (Table 1). Except for these 2 species in 1997, species other than the 3 major species comprised ≥1% of the seed bank only on burned plots immediately after fire where *Bromus* seed densities were greatly reduced (burned plots of the Long Term site in 1996, Table 1; and the Hill site, Table 2). Other species found in the seed bank were another native annual found on the Hill site (Table 2), 4 other introduced annual species, and 3 native perennial shrub-steppe species (Tables 1, 2). Each of these perennials was found only once or twice throughout all the samples.

Seeds of these perennial species are obviously rare, but the 24–40 core samples per plot give a rather crude estimate of seed abundance of species that occur extremely rarely. (One seed occurring throughout 30 cores amounts to 15 seeds $m^{-2}$, and the presence or absence of a species on a plot may be partly due to chance.) A more accurate estimate of the abundance of these perennial-plant seeds involves total number of cores taken across sites and years. The samples from unburned plots of the Long-Term site for each of the 3 years and from the lightly burned Near-Dune site can be combined to represent seed banks of recently unburned *Bromus*-dominated sites. Based on this larger data set (254 core samples), native perennials as a group (excluding *Oenothera pallida*) had a density of 1.9 seeds $m^{-2}$ and made up 0.02% of the seed bank, or about 1 seed in 5000. The burned plots might be considered less likely to contain perennial-plant seeds because part of the seed bank was destroyed by fire. However, of the few perennial-plant seeds that occurred, more were on burned plots. With all burned and unburned plots included (564 cores), perennial-plant seed density was 3.3 seeds $m^{-2}$, or 0.05% of the seed bank.

After the 1995 fire, abundance of *Bromus* seeds on burned plots of the Long-Term site was <3% of that found on unburned plots (Fig. 1). Abundance of *Bromus* seeds on the plots of the Hill site that were burned only in 1995 was similar to that of burned plots of the Long-Term site after the fire, while Hill site plots that were burned in both 1994 and 1995 had *Bromus* seed densities that were lower than on the once-burned plots (Table 2). On the lightly burned Near-Dune site, densities of *Bromus* seeds were much higher than on the Hill site (Table 2), but considerably lower than on unburned plots of the Long-Term site in the same year.

Seed banks were quantified for more than 1 year following fire only on the Long-Term site. Except for the 1-year pulse of *Mentzelia* and *Oenothera* on burned plots after the 1st growing season (Table 1), all species except the 3 dominant annuals occurred only occasionally in the seed banks and played no role in seed bank dynamics. As with *Bromus,* seed banks of the other 2 major annuals were reduced by fire, but less drastically (Table 1). Thus, *Bromus* made up a smaller proportion of the seed bank on the burned plots in 1996 (Table 1). From very low numbers after the fire, the *Bromus* seed bank increased to almost 5000 seeds $m^{-2}$ after just a single growing season, and increased further in the 2nd year (Fig. 1). Densities of *Bromus* seeds on unburned plots were >12,000 $m^{-2}$ in 1996 and 1997 but, for reasons that are unclear, declined greatly in 1998 to levels lower than those of the burned plots in that year (Fig. 1). Seed banks of the other 2 abundant annuals also increased on the burned plots through the first 2 growing seasons following the fire, but more modestly (Fig. 1). After 2 growing seasons, the proportional composition of the seed bank was similar on burned and unburned plots (Table 1).

TABLE 1. Occurrence of the 3 major species and of species infrequently represented in the seed bank for the Long-Term site on unburned plots and on plots burned in late summer 1995. Seed banks in the years 1996, 1997, and 1998 are presented. Three groups of infrequent species are listed: other alien annuals, native annuals, and native perennials. Unknown species are also listed. For each species, mean number of seeds per plot, standardized to number of seeds $m^{-2}$, is presented. The percent of the seed bank occupied by each species is listed in parentheses.

| Species represented in the seed bank | 1996 Unburned No. | 1996 Unburned Percent | 1996 Burned No. | 1996 Burned Percent | 1997 Unburned No. | 1997 Unburned Percent | 1997 Burned No. | 1997 Burned Percent | 1998 Unburned No. | 1998 Unburned Percent | 1998 Burned No. | 1998 Burned Percent |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MAJOR SPECIES | | | | | | | | | | | | |
| *Bromus tectorum* | 12,817 | (92.3) | 333 | (65.7) | 12,806 | (95.3) | 4874 | (81.5) | 6755 | (84.1) | 8650 | (81.4) |
| *Sisymbrium altissimum* | 854 | (5.9) | 130 | (23.1) | 496 | (3.7) | 598 | (10.7) | 932 | (11.0) | 1197 | (11.3) |
| *Salsola iberica* | 244 | (1.8) | 38 | (6.9) | 129 | (1.0) | 256 | (4.5) | 387 | (4.8) | 749 | (7.0) |
| OTHER ALIEN ANNUALS | | | | | | | | | | | | |
| *Lactuca serriola* | 8 | (0.1) | | | | | | | | | 6 | (0.1) |
| *Cirsium* (*Cincus*?) | | | 8 | (1.3) | | | | | | | | |
| *Amaranthus* sp.[a] | | | | | | | 7 | (0.1) | | | | |
| NATIVE ANNUALS | | | | | | | | | | | | |
| *Mentzelia albicaulis* | | | | | | | 103 | (1.5) | | | | |
| *Oenothera pallida* | | | | | | | 90 | (1.3) | | | | |
| NATIVE PERENNIALS | | | | | | | | | | | | |
| *Sporobolus cryptandrus* | | | 8 | (1.3) | | | | | | | | |
| *Chrysothamnus*[b] | | | 8 | (1.7) | | | | | | | | |
| UNKNOWN | | | | | | | | | | | | |
| | | | | | | | 27 | (0.4) | | | 24 | (0.2) |

[a]The *Amaranthus* species was not identified.
[b]*Chrysothamnus* was *C. viscidiflorus*.

TABLE 2. Occurrence of the 3 major species and of species infrequently represented in the seed bank for the Hill site and the Near-Dune site for 1996 only. On the Hill site burn treatments were burned once or twice, as indicated. Three groups of infrequent species are listed: other alien annuals, native annuals, and native perennials. For each species, mean number of seeds per plot, standardized to number of seeds m$^{-2}$, is presented. The percent of the seed bank occupied by each species is listed in parentheses.

| Species represented in the seed bank | Hill site: Burned 1995 No. | Hill site: Burned 1995 Percent | Hill site: Burned 1994, 1995 No. | Hill site: Burned 1994, 1995 Percent | Near-Dune site: Lightly burned 1995 No. | Near-Dune site: Lightly burned 1995 Percent |
|---|---|---|---|---|---|---|
| MAJOR SPECIES | | | | | | |
| *Bromus tectorum* | 289 | (71.0) | 132 | (54.2) | 4827 | (97.1) |
| *Sisymbrium altissimum* | 81 | (20.7) | 95 | (38.1) | 79 | (1.5) |
| *Salsola iberica* | 0 | (0) | 0 | (0) | 59 | (1.2) |
| OTHER ALIEN ANNUALS | | | | | | |
| *Lactuca serriola* | | | 10 | (3.6) | | |
| *Erodium cicutarium* | 21 | (5.6) | | | | |
| NATIVE ANNUAL | | | | | | |
| *Gilia* spp.[a] | 10 | (2.8) | | | | |
| NATIVE PERENNIALS | | | | | | |
| *Sporobolus cryptandrus* | | | | | 1 | (0.2) |
| *Sphaeralcea munroana* | | | 9 | (4.2) | | |

[a]The *Gilia* species was either *G. leptomeria* or *G. inconspicua.*

## DISCUSSION

This study indicates that an extremely sparse perennial-plant seed bank occurs in *Bromus*-dominated communities. Individual perennial species often have seed banks of only 1–5 seeds m$^{-2}$ in perennial-dominated shrub-steppe communities (Hassan and West 1986), although seed banks of some perennial species may be considerably larger at some times of year (e.g., *Chrysothamnus viscidiflorus* in autumn; Young and Evans 1975). However, the total perennial-plant seed bank in our experiment, 2–3 seeds m$^{-2}$ with only 3 species represented, contrasts with the perennial-plant seed bank of an unburned shrub-steppe community described by Hassan and West (1986): 25–27 seeds m$^{-2}$ representing 8–13 perennial species. Two of the 4 perennial plant seeds we identified were of the grass *Sporobolus cryptandrus*, which is known to form a persistent seed bank (Lippert and Hopkins 1950) that would allow it to remain longer in the seed bank of *Bromus*-dominated communities after *Sporobolus* plants were gone. A 2nd perennial in the seed bank, *Sphaeralcea munroana,* probably also forms a persistent seed bank (see Roth et al. 1987). Since some seeds of such species could have remained dormant through our germination trials, density of this persistent seed bank could be higher than the extremely low levels indicated by our data. The 3rd perennial, *Chrysothamnus viscidiflorus,* forms no persistent seed bank (Meyer and McArthur 1987) but has wind-dispersed achenes, so the seed found apparently entered the plot from plants near the site. Germination trials were less likely to underestimate densities of nondormant seeds such as those of *Chrysothamnus.* The virtual absence of these formerly dominant species from the seed bank is a major obstacle to their reestablishment. Similarly, reestablishment of late-successional grasses of savannahs of the Edwards Plateau of Texas was impaired by absence of these species from the seed bank (Kinucan and Smeins 1992).

Except on plots where fire had recently consumed most seeds, densities of *Bromus* seeds were similar to or higher than those reported by others (5900 m$^{-2}$, Stewart and Hull 1949; 2400–8300 m$^{-2}$, Young and Evans 1975; 10,000–15,000 m$^{-2}$, Young and Evans 1985). Hassan and West (1986) reported a 3.5-fold increase in the *Bromus* seed bank after 1 growing season following a fire. The increase in *Bromus* seed bank after fire in this study was even greater. The amount of the *Bromus* seed bank destroyed by fire varies depending on the intensity of the fire. The fire on the Long-Term site consumed almost all litter on the plots, and the *Bromus* seed bank that remained was <3% that of unburned plots. Yet, even after this great reduction, the *Bromus* seed bank recovered to high levels after only 1 growing season. Young and Evans (1985) reported that *Bromus* can recover to high densities

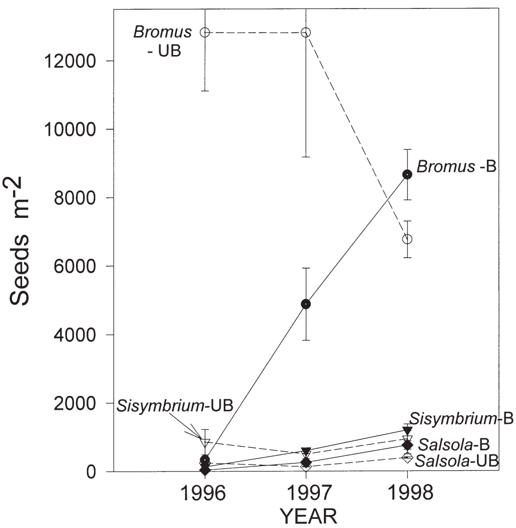


Fig. 1. Number of seeds $m^{-2}$ (means of the 2 plots and standard errors) of each of the 3 major species, *Bromus tectorum, Sisymbrium altissimum,* and *Salsola iberica,* on plots burned (B) and unburned (UB) in 1995 on the Long-Term site in each of the 3 years of the experiment. Filled symbols represent burned plots; open symbols represent unburned plots.

within 3 years following fire. On the Long-Term site *Bromus* seed banks recovered to essentially pre-burn levels in the same amount of time.

Although fire reduced abundance of *Bromus* seeds for 1 year, *Bromus* never lost dominance of the seed bank. Its dominance was somewhat decreased immediately after the fire, with seeds of *Sisymbrium* and *Salsola* becoming proportionally more abundant, but *Bromus* quickly returned to its previous level of dominance. The fire and resulting reduction in abundance of *Bromus* seeds on the Long-Term site appeared to provide some opportunity for 2 native species, *Mentzelia* (annual) and *Oenothera* (annual to short-lived perennial), to establish, but they were only transitory as a substantial component of the seed bank. *Mentzelia* apparently can form a persistent seed bank (Henderson et al. 1988). A small persistent seed bank of these species may have been present at the time of the fire, although none was detected in the 1996 samples.

There were too few perennial-plant seeds to determine differences in their abundances between burn treatments or years. Apparently, only very small numbers of seeds of native perennials that form a persistent seed bank remained in the *Bromus*-dominated communities, and dispersal of perennial-plant seeds onto the site appeared extremely rare. Despite the reduction in abundance of *Bromus* seeds after fire, seeds of perennials were so few that seeds of *Bromus* and other introduced annuals still outnumbered seeds of perennial plants by orders of magnitude, and no opportunities for changes in species composition to perennial plants were created.

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