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Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland

Robert D. Cox · Edith B. Allen

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Abstract Soil seed banks are important to many plant communities and are recognized as an important component of management plans. Understanding seed bank composition and density is especially important when communities have been invaded by exotic species and must be managed to promote desirable species. We examined germinable soil seed banks in southern California coastal sage scrub (CSS) that is heavily invaded by exotic grasses and in adjacent exotic grassland. Soils from both communities had similar seed banks, dominated by high densities of exotic grass and forb species. Up to 4,000 exotic grass seeds and at least 400 exotic forb seeds/m^2 were found in most soils, regardless of aboveground vegetation type. Native forbs averaged 400 seeds/m^2 in grass-dominated areas and about 800 in shrub-dominated soils. Shrub seed density was <1 and <10 seeds/m^2 in grass- and shrub-dominated areas, respectively, indicating that the shrub seed bank is not persistent compared to annuals. We also compared pre- and post-burn soil seed banks from one location that burned in October 2003. Late-season burning in both grass- and CSS-dominated areas disproportionately reduced exotic grass seed densities relative to native seed densities. The similarity of the seed banks in adjacent grass and shrub communities suggests that without intervention, areas currently dominated by CSS may become more similar to grass-dominated areas in terms of aboveground vegetation. In such areas, the first growing season following a wildfire is a window of opportunity for increasing native diversity at a time when density of exotic grass seeds is low.

Keywords *Bromus* · Disturbance · Ecological management · *Erodium* · Invasive species · Wildfire

Introduction

Soil seed banks are integral to many plant communities (Major and Pyott 1966; Roberts 1981; Coffin and Lauenroth 1989; Holmes and Newton 2004; James et al. 2007), but because they are not immediately observable their importance may be overlooked. The composition of the soil seed bank, defined as the group of viable seeds stored in the soil (Roberts 1981), is related to composition of the aboveground vegetation over time, its seed production, and how long each seed persists in the soil (van der Valk and Pederson 1989). Characterization

At time of research, Robert D. Cox was graduate student.

R. D. Cox (✉)
US Forest Service Rocky Mountain Research Station,
322 E. Front St., Suite 401, Boise, ID 83702, USA
e-mail: robdcox@gmail.com

R. D. Cox · E. B. Allen
Department of Botany and Plant Sciences,
University of California, Riverside, CA 92521, USA

of a seed bank can also give some idea of the future of the community, since it represents not only a partial record of previous plants at the site, but also part of the plant community's response to changing conditions through time (Templeton and Levin 1979; Coffin and Lauenroth 1989; van der Valk and Pederson 1989; Auld and Denham 2006).

Throughout the western U.S., invasion of exotic annual plants into semi-arid shrub ecosystems has resulted in the conversion of large areas into stable communities dominated by annual grasses of Mediterranean origin (Mack 1981; D'Antonio and Vitousek 1992; DiTomaso 2000; Pimentel et al. 2005). Even without complete conversion, invaded plant communities experience altered fire regimes and loss of biodiversity (D'Antonio and Vitousek 1992; Mack and D'Antonio 1998), and are often targets for conservation and restoration (Bowler 1990; Pellant et al. 2004). One critical aspect of both restoration and conservation in these areas is the status of the soil seed bank (Major and Pyott 1966; Keddy et al. 1989; van der Valk and Pederson 1989; Holl et al. 2000; Roovers et al. 2006; Wearne and Morgan 2006). Although changes in aboveground vegetation after invasion are well documented, little research has addressed the issue of post-invasion changes in the seed bank. However, seed banks in these areas likely experience profound changes that mirror changes in the aboveground portion of the plant community (Cione et al. 2002; Navie et al. 2004).

Since seed banks in many Mediterranean-type ecosystems are persistent (Parker and Kelly 1989), long-lived seeds of some native species may persist in soils beneath grass-dominated communities even when native species are absent aboveground. In addition, since soil-stored seed represents part of the community's response to disturbances, including climatic events and even management and restoration efforts (Coffin and Lauenroth 1989; van der Valk and Pederson 1989; Auld and Denham 2006), seed bank differences between communities that have experienced vegetation-type conversion and adjacent communities that have been invaded but not yet converted are of particular interest. Similarities in such seed banks may indicate a potential for similar responses to future disturbance, even if aboveground plant communities are dissimilar.

One semi-arid shrub community that has been extensively invaded by exotic annual grasses is southern California coastal sage scrub (CSS) (O'Leary 1995; Minnich and Dezzani 1998; Sirulnik et al. 2007). CSS vegetation consists of a diverse assemblage of drought-deciduous and seasonally dimorphic shrubs and subshrubs, and a rich understory of herbaceous annuals (Westman 1981, 1983, 1987; O'Leary et al. 1992; DeSimone 1995). CSS also harbors a high number of endangered, threatened, and "special concern" species (O'Leary et al. 1992; Bowler 2000; CNPS 2001), but has suffered widespread type conversion and degradation through invasion of exotic species (Klopatek et al. 1979; Westman 1981; O'Leary 1995; Minnich and Dezzani 1998).

Conversion and degradation of CSS are driven by threats on several fronts, such as development of private property (O'Leary 1995), nitrogen deposition and other forms of air pollution (Westman 1985; Fenn et al. 2003), fragmentation (O'Leary 1995; Zink et al. 1995), and reduced fire return intervals (Zedler et al. 1983; Keeley 1986; Minnich and Dezzani 1998). These threats are ongoing and are likely contributing to the degradation of the little CSS that has survived to the present by encouraging invasion of exotic grasses (O'Leary 1995; Minnich and Dezzani 1998; Bowler 2000; Cione et al. 2002). For these reasons, concern is growing over CSS decline and associated loss of biodiversity (Bowler 2000). These concerns, combined with political and policy imperatives, have made preservation and restoration of CSS vegetation a high priority for land managers (Bowler 2000; Rubinoff 2001).

The status of the seed bank in CSS communities, though often overlooked, is likely to be crucial to management of these areas. Indeed, as Major and Pyott (1966) point out, description of a plant community is incomplete without an understanding of the soil seed bank. Although little research has directly investigated the issue of seed bank changes in heavily invaded CSS areas, evidence exists for such changes, including complete native seed bank loss due to frequent fire (Cione et al. 2002). Some studies have investigated seed banks in CSS (Keeley and Keeley 1984) and related vegetation types such as coastal succulent scrub (Angoa-Roman et al. 2005), chaparral (Zammit and Zedler 1994; Holl et al. 2000), and grassland (Major and Pyott 1966), but estimates of seed density have varied widely. This may be due to

both the high degree of spatial and temporal heterogeneity associated with some seed banks (Henderson et al. 1988; Coffin and Lauenroth 1989; Wilson et al. 2004) and to different sampling techniques (Roberts 1981; Cardina and Sparrow 1996; Ishikawa-Goto and Tsuyuzaki 2004; Devictor et al. in press). Nevertheless, an understanding of the status of the seed bank in CSS and adjacent grassland areas will provide valuable information about the future of CSS (van der Valk and Pederson 1989). For CSS areas established as habitat preserves, such information will be necessary to ensure preservation.

We sampled the seed bank at three locations in a CSS habitat preserve in western Riverside County, California. Differences between CSS and adjacent exotic grassland seed banks were observed by allowing the soil-stored seeds to germinate in a glasshouse and identifying the germinants. We also observed seed bank differences between pre-burn and post-burn soils when one CSS location burned in a wildfire in October 2003.

Methods

Study site

The Shipley Reserve (33°39′18″ N, 116°59′49″ W) was established within the Western Riverside County Multi-species Habitat Reserve, California, in 1992 to provide habitat connectivity between two reservoirs. The reserve provides chaparral, oak woodland, and CSS vegetation areas for conservation. CSS portions of the reserve, now restricted to hills and slopes, are heavily invaded by annual grasses and forbs, including *Avena fatua* L., *Bromus diandrus* Roth, *B. hordeaceus* L., *B. madritensis* L. subsp. *rubens* (L.) Husn., *Erodium brachycarpum* (Godr.) Thell., *E. cicutarium* (L.) Aiton, and *Hirschfeldia incana* (L.) Lagr.-Fossat (nomenclature follows Hickman 1993). Shrub density in CSS areas studied ranged from 0.12 to 0.52 shrubs/m^2, and consisted mainly of *Eriogonum fasciculatum* (Benth.) Torr. & A. Gray, and *Artemisia californica* Less., with *Salvia apiana* Jeps., *Keckiella antirrhinoides* (Benth.) Straw, with other species also present. Interspersed between hillside CSS patches are valley bottoms that were formerly cleared of shrubs and are now composed mostly of dense exotic grasses and forbs (Allen et al. 2005).

Seed bank sampling

We selected three locations on the reserve with similar topography and vegetation and took soil samples from 30 × 30 m plots in adjacent CSS- and exotic grass-dominated areas at each location. CSS areas sampled occurred on approximately N-facing slopes (about 10% slope), and grass areas were located on level ground at the base of each CSS-dominated slope. Within each plot, soil samples were collected in a stratified random manner, using a 10 cm-diameter soil corer inserted 7 cm into the soil. In October 2003, 30 samples were taken in each vegetation type at each location for a total of 180 samples and a total volume of more than 98,000 cm^3. Soils were sampled again in October 2004, from the same areas and in the same manner, except that 50 samples were taken from each area for a total of 300 samples and more than 164,000 cm^3 of soil. Each sample was air dried and stored at about 4°C until soils were transferred to a greenhouse for germination.

In late October 2003, wildfires burned approximately 1,600 ha on the Shipley Reserve, including one site (one grass- and one shrub-dominated plot) from which soil samples had been collected approximately two weeks earlier. Following the fire, soils in these plots were resampled to allow statistical inference between burned and unburned soils.

In October 2004, about four days before any samples were taken, early rains fell in the area, wetting the soil and stimulating germination. When samples were taken from the field, all germinated seedlings were recorded and removed. These seedlings were included in subsequent analyses. The soil was then dried, taken to the glasshouse, and any emerging seedlings were also recorded.

Glasshouse seedling emergence was used to quantify germinable seed bank composition and density (Roberts 1981; Simpson et al. 1989). Beginning in March following each year's sample collection, samples were spread to a depth of about 1.5 cm on 20 × 20 cm trays in a glasshouse with ambient light. Glasshouse temperatures were maintained between 18 and 26°C. Each sample was kept moist, and emerging seedlings were identified and removed. Unidentifiable seedlings were removed, transplanted to a separate pot, and grown until they were identifiable. When emergence was zero for

several days, soils were allowed to dry, stirred by hand, and rewetted. Emerging seedlings were again identified and removed. This was repeated until no seedlings emerged, usually the third cycle. Cycles ranged in length from 4 to 7 weeks.

Data analysis

For analysis, species were grouped into exotic grass, exotic forb, native forb, and native shrub species groups. Species present in more than 20% of samples overall were also analyzed individually. Data were square root transformed and analyzed in JMP (SAS Institute 2006) using ANOVA and Tukey's HSD to compare differences between years, locations, and vegetation types, and to compare burned versus unburned areas. Since only one site (site 3) burned, samples from the unburned soils (sites 1–3) were analyzed together, and then site three (burned and unburned) was analyzed separately to evaluate the effects of wildfire on the soil seed bank.

Results

A total of 35,882 seedlings belonging to at least 40 species germinated during this study for an average of 12,643.1 seedlings/m^2 in exotic grass areas and 6,023.5 seedlings/m^2 in CSS areas. Unburned soils held an average of 9,031.6 seeds/m^2 and burned soils had 1,288.3. Overall there were seven exotic grass species, eight exotic forbs, two native shrubs, one native grass, and 21 native forbs (Table 1). At most locations, seed densities were similar between grass and CSS areas although some species did have greater density in one or the other type. In addition, burned soils had fewer total seedlings than unburned soils, especially of exotic grasses. Only a few species were present in greater than 20% of the soil samples and were analyzed individually; these species are indicated in bold in Table 1.

Exotic grass seedlings were very numerous in all soils, regardless of year, location, or aboveground plant community, but did exhibit a vegetation type by site interaction (Fig. 1). Soils from site one had more than 10,000 exotic grass seedlings germinate per m^2 in soils from the grass-dominated area, and only about 1,500 seedlings/m^2 in soils from the shrub-dominated area. Soils from other sites did not differ; all had about 4,000 exotic grass seedlings in both grass- and shrub-dominated areas. Patterns did not differ between 2003 and 2004.

Exotic forbs had a 3-way interaction of year by vegetation type by site (Fig. 2). In 2003, site one had more exotic forb seedlings in soils from exotic grass-dominated areas than from shrub-dominated soils. The difference was much more pronounced in samples taken in 2004, when soils from all three grass-dominated sites had much larger densities of seedlings than soils from the shrub sites. Nevertheless, even though exotic forb seedlings were less numerous than exotic grass seedlings in most soils, they still achieved high densities. Even the shrub-dominated areas, which had fewer exotic forb seedlings, had at least 400 m^{-2}.

Seedlings of native forbs exhibited a three-way interaction of year by habitat by site (Fig. 3). Overall, soils collected in 2004 had more native seedlings per m^2 than soils collected in 2003. Soils collected in 2004 from the shrub-dominated area of site three had higher native seedling density than all other soils. Soils collected in 2003 all had similar levels of native forbs, averaging about 150 seedlings/m^2. Native shrub seedlings were much less numerous in both grass- and shrub-dominated soils than the other species groups. Across both years, grass-dominated soils averaged less than one seedling per m^2, while shrub-dominated soils averaged almost seven (data not shown).

Burning the aboveground vegetation influenced the composition of the soil seed bank (Fig. 4). Soils that were sampled immediately after the fire had fewer seedlings of exotic grasses than soils taken from the same area prior to burning, regardless of aboveground vegetation type. After 1 year, however, density of exotic grass seeds had partially recovered. Exotic and native forb seedlings were not reduced in burned soils sampled in 2003 compared to unburned soils, but exotic forb seedlings were more numerous in soils sampled in 2004.

Discussion

Analysis of seed banks at the Shipley Reserve shows that adjacent grass- and shrub-dominated areas are

Table 1 Species, total number of seedlings emerging, and average density per m^2 in soils collected in 2003 and 2004 at the Shipley Reserve in Riverside County, CA

Family	Species	# of seedlings	Average seedlings per m^2			
			Grass	Shrub	Unburned	Burned
	Exotic grasses	21,224	7,261.2	3,932.2	7,338.9	146.7
	Avena barbata	178	93.0	1.1	2.1	0.0
	Bromus diandrus	1,159	**569.0**	42.4	**1,473.6**	4.3
	Bromus hordeaceous	5,275	**1,975.9**	805.9	**1,974.6**	34.5
	Bromus madritensis* ssp. *rubens	11,976	**4,084.9**	2,235.6	**2,836.6**	64.7
	Hordeum murinum	8	2.1	0.0	4.2	8.6
	Schismus barbatus	1,127	30.1	560.2	924.7	30.2
	Vulpia myuros	1,501	506.1	287.0	123.1	4.3
	Exotic forbs	11,494	4,713.6	1,126.3	1,440.2	969.0
Amaranthaceae	*Amaranthus albus*	9	3.2	1.1	4.2	2.2
Asteraceae	*Filago gallica*	66	5.3	29.7	0.0	0.0
	Hypochaeris glabra	120	39.1	23.3	83.5	4.3
	Lactuca serriola	3	0.5	1.1	0.0	0.0
Brassicaceae	*Hirschfeldia incana*	23	9.5	1.6	2.1	4.3
	Sisymbrium irio	395	197.1	10.1	25.0	6.5
Geraniaceae	***Erodium brachycarpum***	9,707	**4,343.8**	551.7	**1,237.8**	919.3
	Erodium cicutarium	1,171	105.1	**507.7**	87.7	32.4
	Native forbs	2,335	407.3	800.0	210.8	120.8
Apiaceae	*Daucus pusillus*	2	0.0	1.1	0.0	0.0
Asteraceae	*Hemizonia kelloggii*	8	3.7	0.5	0.0	0.0
Boraginaceae	*Amsinckia menziesii*	158	80.8	1.6	2.1	4.3
	Cryptantha intermedia	124	1.6	64.2	0.0	0.0
Brassicaceae	*Calyptridium monandrum*	3	0.0	0.5	0.0	4.3
Euphorbiaceae	*Chamaesyce albomarginata*	1	0.5	0.0	0.0	0.0
	Eremocarpus setigerus	297	**140.5**	6.9	150.3	38.8
Fabaceae	*Lotus scoparius*	92	6.3	41.9	2.1	2.2
	Lotus strigosus	44	0.5	22.3	0.0	2.2
	Lupinus sparsiflorus	1	0.0	0.5	0.0	0.0
	Lupinus truncatus	2	0.0	1.1	0.0	0.0
	Trifolium spp.	14	1.1	6.4	0.0	0.0
Lamiaceae	*Salvia columbariae*	3	0.0	1.6	0.0	0.0
	Trichostema lanceolatum	11	1.1	4.8	0.0	0.0
Lilliaceae	*Dichelostemma capitatum*	44	4.2	18.6	0.0	2.2
Onagraceae	*Clarkia purpurea*	12	3.7	2.7	2.1	0.0
Polemoniaceae	***Gilia angelensis***	1,338	145.8	**557.0**	27.1	25.9
Portulacaceae	*Calandrinia ciliata*	176	17.4	65.8	27.1	41.0
	Calystegia macrostegia	3	0.0	1.6	0.0	0.0
Scrophulariaceae	*Antirrhinum coulterianum*	1	0.0	0.5	0.0	0.0
Violaceae	*Viola pedunculata*	1	0.0	0.5	0.0	0.0
	Unknown species	813	259.4	158.1	35.5	51.8
	Native shrubs	14	0.5	6.9	6.3	0.0
Asteraceae	*Artemisia californica*	5	0.0	2.7	0.0	0.0

Table 1 continued

Family	Species	# of seedlings	Average seedlings per m^2			
			Grass	Shrub	Unburned	Burned
Polygonaceae	*Eriogonum fasciculatum*	9	0.5	4.2	6.3	0.0
	Native Grass	2	1.1	0.0	0.0	0.0
Poaceae	*Nassella pulchra*	2	1.1	0.0	0.0	0.0
	Total	35,882	12,643.1	6,023.5	9,031.6	1,288.3

Data averaged over sites and years. Species and numbers in bold indicate significantly higher density between grass- and shrub-dominated areas or between the unburned and burned soils from site 3 in 2003 for those species present in more than 20% of samples. Nomenclature follows Hickman (1993)

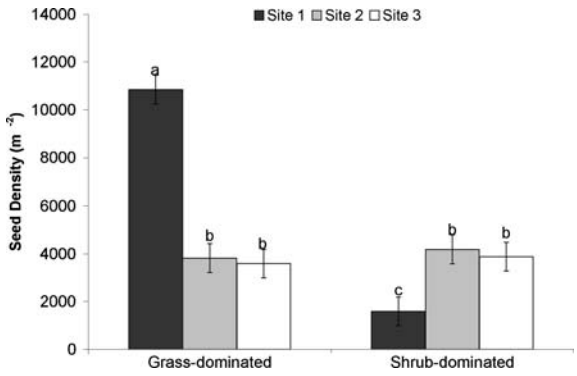

Fig. 1 Number of exotic grass seeds per m^2 in unburned soils averaged over 2003 and 2004 from adjacent vegetation types at three locations in the Shipley Reserve, Riverside County, CA. Lowercase letters indicate significant differences ($P = 0.05$). Bars indicate standard error

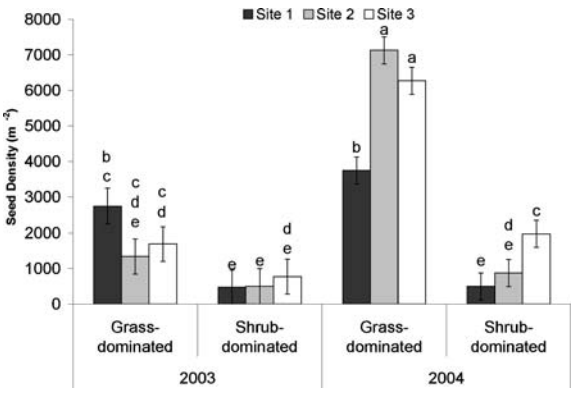

Fig. 2 Number of exotic forb seeds per m^2 in unburned soils collected in 2003 and 2004 from adjacent vegetation types at three locations in the Shipley Reserve, Riverside County, CA. Lowercase letters indicate significant differences ($P = 0.05$). Bars indicate standard error

both filled with seeds of exotic species. There were few differences between most grass- and shrub-dominated areas in terms of numbers of exotic grass seeds; all had high densities. Although the shrub-dominated area of site one had fewer seeds than the adjacent grass-dominated area, these soils still had more than 1,500 exotic grass seeds per m^2. Exotic forb seeds were more numerous in grass than shrub areas, although shrub areas had at least 466 seeds/m^2. Even the lower densities of exotic seeds observed in shrub-dominated areas are still overwhelming compared to native seed and seem likely to permit increasing domination of these sites by exotic species. The shrub seed density is especially low even in shrub-dominated areas, consistent with other observations that the native annual seedbank is more persistent than the shrub seedbank (Keeley and Keeley 1984). Evidence also exists that shrub seeds are quickly depleted from the seed bank in areas experiencing frequent wildfires fueled by annual grasses (Cione et al. 2002).

The similarity of the adjacent communities' seed banks poses significant questions for the future of CSS vegetation at these sites. The annual portion of the seed bank can be a suitable predictor of the annual portion of the aboveground plant community in vegetation types similar to CSS (Henderson et al. 1988; Olano et al. 2005). Since the soil seed bank is a component of the community's ability to respond to disturbance (Templeton and Levin 1979; Coffin and Lauenroth 1989; Auld and Denham 2006), the similarity between these communities' seed banks indicates that they are likely to have similar responses to disturbances. In this case it is probable that without careful management efforts, CSS areas could become more similar to the adjacent grass-dominated areas

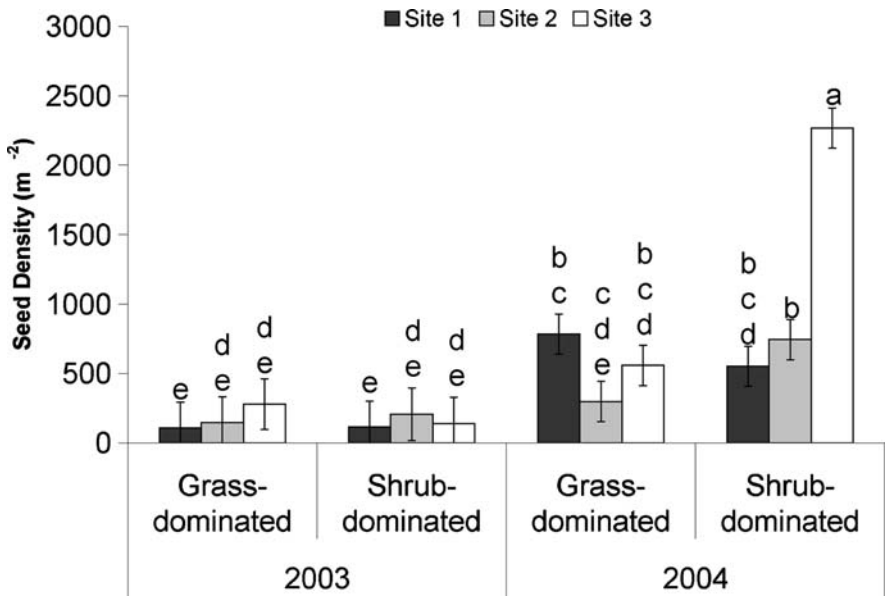

Fig. 3 Number of native forb seeds per m^2 in unburned soils collected in 2003 and 2004 from adjacent vegetation types at three locations in the Shipley Reserve, Riverside County, CA. Lowercase letters indicate significant differences ($P = 0.05$). Bars indicate standard error

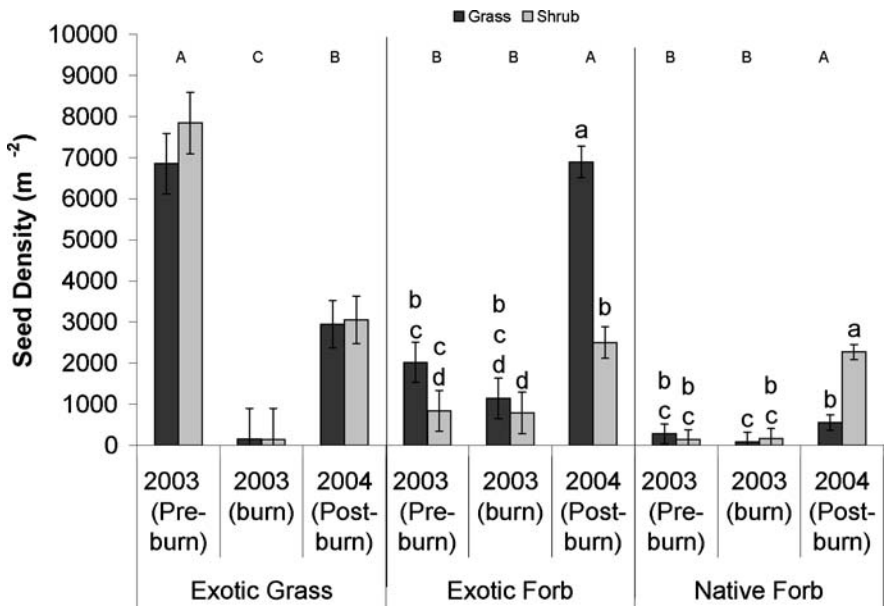

Fig. 4 Number of exotic grass, exotic forb, and native forb seeds per m^2 in soils collected in 2003 before and after an October wildfire, and in 2004, 1 year following the wildfire in adjacent vegetation types in the Shipley Reserve, Riverside County, CA. Lowercase letters indicate within species group significant differences ($P = 0.05$). Bars indicate standard error

after disturbance. Such management efforts will be greatly influenced by the state of the soil seed bank and therefore, must incorporate analysis of these seed banks to determine appropriate actions (Major and Pyott 1966; van der Valk and Pederson 1989; Fahnestock et al. 2003; Hesse et al. 2007; Robertson and James 2007).

Other estimates of seed bank density in CSS, grassland, and similar habitats have produced widely varied numbers. Keeley and Keeley (1984) used in situ germination to estimate that CSS vegetation near Los Angeles, CA, had about 3,000 seeds/m^2; in mixed chaparral, Zammit and Zedler (1994) and Holl et al. (2000) both used greenhouse germination

and found almost 6,000 seeds/m^2 and more than 20,000 seeds/m^2, respectively; Angoa-Roman et al. (2005) used a dissecting microscope to sort and count seeds, and found about 12,000 seeds/m^2 in coastal scrub in Baja California; Major and Pyott (1966) estimated 8,000–12,000 seeds/m^2 in northern California grasslands by using greenhouse germination. Since estimates of seed bank density are known to vary with sampling method (Roberts 1981; Cardina and Sparrow 1996), as well as in time and space (Henderson et al. 1988; Coffin and Lauenroth 1989), the wide range in seed bank estimates is not surprising. We also observed high temporal and geographic variation. Nevertheless the consistently high numbers of exotic seeds relative to native seeds in this analysis suggest that native species in these areas face a considerable obstacle in establishing from a seed bank that is overpopulated with seeds of exotic, competitive species.

Fire is known to exert a large influence on soil seed banks (Mueggler 1956; Zammitt and Zedler 1988), and factors such as soil heating, wood charate, and smoke may alter the relative composition and total density of the seed bank (Keeley 1987; Keeley and Keeley 1987; Zammit and Zedler 1988, 1994; Roche et al. 1998; Holl et al. 2000; Coates 2003; Hill and French 2003). In this study a late-season fire disproportionately influenced seed bank composition, severely reducing the density of exotic grass seedlings while not significantly changing the density of native forb seeds. The effects of fire on a seed bank are sensitive to the timing and frequency of the treatment (Roche et al. 1998). Almost yearly fall fires eliminated the native seed bank in one former CSS site (Cione et al. 2002). Where fire can be better controlled, our results suggest the possibility that seed banks in CSS and adjacent grassland areas might be amenable to direct manipulation by management activities such as prescribed burning (Keddy et al. 1989; van der Valk and Pederson 1989; Chambers and MacMahon 1994). Indeed, prescribed spring burning has been applied successfully to eliminate grass seeds before shattering occurs and is still the most logistically feasible burning treatment (Young et al. 1981; Meyer and Schiffman 1999; Gillespie and Allen 2004; DiTomaso et al. 2006). Nevertheless even when burning is unplanned, such as the fall wildfire in this study, the first growing season following the wildfire is a window of opportunity for increasing native diversity at a time when the exotic grass seed bank has been reduced. However, such a window may be open only a short time, as exotic seed banks began to recover within one season after the fire.

In an optimistic view on the potential for restoration of invaded California grasslands, Seabloom et al. (2003) suggested that augmenting the native seed bank could be a successful strategy. However, this does not take into account the overwhelming ability of the exotic grasses to contribute to the seed bank compared to native species. The composition of soil seed banks observed in this study suggests that heavily invaded CSS areas that have not yet experienced type-conversion are likely to convert in the future following disturbance. Other researchers have predicted the eventual conversion and loss of most CSS as well, based on anthropogenic disturbances such as frequent fire, nitrogen deposition, or urbanization (Minnich and Dezzani 1998; Sirulnik et al. 2007; Syphard et al. 2007). The soil seed banks observed in this study support those predictions. Soil samples had similar numbers of exotic species, regardless of existing plant community. Burning of the aboveground vegetation did influence the composition of the soil seed bank in this study and may provide a window of opportunity for restoration when exotics are low in seed density. Other studies suggest spring burning is more effective in reducing exotic annuals and increasing natives (DiTomaso et al. 1999, 2006; Gillespie and Allen 2004), but these did not include seed bank analysis.

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