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Effects of seeding ryegrass (*Lolium multiflorum*) on vegetation recovery following fire in a ponderosa pine (*Pinus ponderosa*) forest*

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Abstract. Forty-nine vegetation transects were measured in 1997 and 1998 to determine the impact of grass seeding after the 1996 Dome Fire, which burned almost 6900 ha of ponderosa pine (*Pinus ponderosa* Lawson) forest in the Jemez Mountains of north-central New Mexico. High- and moderate-burned areas in Santa Fe National Forest were seeded with a mixture that included the exotic ryegrass (*Lolium multiflorum* Lam.). Adjacent burned areas of Bandelier National Monument were not seeded, and were used as a control in the post-seeding study. On the seeded plots, foliar cover of ryegrass declined from 1997 to 1998 due to self-inhibition and/or reduced precipitation from 1997 to 1998. Foliar cover and diversity of native forbs were greater in 1997 than 1998, probably due to a wet growing season in 1997. Cover, species richness, and diversity of native forbs were highest in non-seeded areas of moderate- and high-burn intensities. Regeneration and survivorship of conifer seedlings decreased as ryegrass cover increased, particularly in areas of high-burn intensity. Exotic plant cover, mostly horseweed [*Conyza canadensis* (L.) Cronq.], increased from 1997 to 1998 in non-seeded areas of moderate- and high-burn intensity. Both the initial success of seeding and the eventual impacts on native vegetation were strongly modulated by climate variability.

Additional keywords: south-western USA; New Mexico; burn intensity; *Conyza canadensis*; diversity; exotics; post-fire rehabilitation.

Introduction

Presettlement natural fire intervals ranged from 2 to 15 years in ponderosa pine (*Pinus ponderosa* Lawson) forests across the south-western USA (Swetnam and Baisan 1996; Swetnam and Betancourt 1998), including the Jemez Mountains in northern New Mexico (Touchan *et al*. 1996). Since the late 1800s, however, widespread, low-intensity surface fires ceased across most of this region due to reduction of fine fuels with intense livestock grazing and proactive fire suppression after World War II (Swetnam *et al*. 1999; Allen 2002). This gradual change in land use and management converted open ‘parklands’ to dense thickets of ponderosa pine, establishing conditions for high-intensity crown fires (Cooper 1960; Allen 1989; Covington and Moore 1994; Allen *et al*. 2002).

Vegetation loss after a catastrophic fire has the potential to increase runoff, erosion and sediment transport while affecting other biological, geomorphic and hydrological processes (e.g. Cannon and Reneau 2000; Moody and Martin 2001; Veenhuis 2002). Costly post-fire rehabilitation practices, such as seeding with non-native species, have been applied by land managers for more than a century, yet remain controversial (Everett *et al*. 1990). Burned areas sometimes are seeded because regrowth of native species may be too slow, or density of surviving plants too sparse, to maintain soil stability and restore nutrient cycles (Tiedemann and Klock 1976; Taskey *et al*. 1989). Grasses are used most often in seeding because they establish easily and colonize disturbed sites rapidly (Everett *et al*. 1990). Experiments assessing the effects of seeding have provided conflicting results, including reduced erosion (Roby 1989), no effect on erosion (Roby 1989), and variable success controlling erosion depending on aspect and elevation (Wakimoto 1979; Miles *et al*. 1989).

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A recent synthesis of the effectiveness of post-fire rehabilitation treatments concluded that seeded grasses are not effective in curbing erosion in the first year after seeding (Robichaud *et al*. 2000). This is particularly a problem in the monsoonal south-western USA, where there is always a high probability of intense thunderstorms in July and August, at the end of a long fire season. Also, an increase in long-term erosion could occur in the lull between the decline of seeded grasses and recovery of native vegetation (Nadkarni and Odion 1986), particularly if nitrogen depletion or shading by exotic plants species inhibit succession by native species.

As part of Burned Area Emergency Rehabilitation (BAER) efforts, exotic plant species such as ryegrass (*Lolium multiflorum* Lam.) often are used for seeding, but effects on native plants are rarely monitored or published in the primary literature (for exceptions, see Griffin 1982; Conard *et al*. 1991). Planting ryegrass has reduced biomass, diversity, and species richness of native plants (Nadkarni and Odion 1986; Conard *et al*. 1991), and may also inhibit native successional species, including annuals and shrubs, through competition for nitrogen (Dodge 1979; Wakimoto 1979). Opponents of ryegrass seeding argue that the species is a strong competitor for water, nutrients, light, and growing space and may have allelopathic properties that could inhibit native species. Although it is only transient in the ecosystem, ryegrass may have long-term effects, such as interfering with the development of deep-rooting native plants essential for long-term protection of watersheds (Corbett and Rice 1966; Hanes 1971; Biswell 1974; Arndt 1979; Wakimoto 1979; Keeley *et al*. 1981; Gautier 1982; Griffin 1982; Zedler *et al*. 1983; Nadkarni and Odion 1986; Conard *et al*. 1991). In addition, the inevitable presence of contaminants introduces undesirable weedy plants when applying large quantities of seed across extensive burn areas. Seeding proponents agree that ryegrass may interfere with native species, but may not threaten long-term functionality of ecosystems because it leaves the system within 3–5 years of initial seeding (Schultz *et al*. 1955; Krammes and Hill 1963; Corbett and Green 1965; Biswell 1974; Conrad 1979; Dodge 1979; Kay *et al*. 1981; Gautier 1982).

Short- and long-term effects of seeded vegetation on soil erosion, nutrient cycling, and succession of native plants remain uncertain, in particular the effects of ryegrass in ponderosa pine ecosystems. Where ryegrass was used to seed after fire in central California, naturally regenerated ponderosa pine seedlings had lower survivorship in seeded than in non-seeded plots (Griffin 1982). Similarly, following wildfires in the Sierra Nevada Mountains, increased ryegrass cover was associated with decreased density of ponderosa pine seedlings. Cover of native herbaceous vegetation and shrub seedling density also decreased as cover of ryegrass increased (Conard *et al*. 1991). Finally, both the success of seeding and long-term recovery of native vegetation likely depends in large part on climatic conditions, which vary in space and time.

Here, we report on a post-seeding study related to the Dome Fire, which in May 1996 burned 6900 ha of ponderosa pine in the Jemez Mountains of north-central New Mexico. The general purpose of the study was to examine the effects of burn intensity and seeding with ryegrass on the recovery of vegetation following wildfire. Specific objectives were (1) to assess the influence of burn intensity on ryegrass success; (2) determine effects of treatments (i.e. seeding with ryegrass and burn intensity) on cover, richness, and diversity of native forbs; (3) assess the influence of treatments on regeneration and survivorship of conifer seedlings; and (4) examine the response of exotic plant species to treatments after accounting for year and site effects (e.g. region, elevation, and moisture index).

Environmental setting

The Dome Fire (25 April to 3 May 1996) burned hillslopes at 2068–2668 m in the Jemez Mountains, across adjacent areas of Bandelier National Monument (BNM) and Santa Fe National Forest (SFNF) (35°26′ N, 106°22′ W) (Fig. 1). Pre-fire vegetation was predominantly ponderosa pine forest grading into mixed-conifer forest (e.g. Douglas fir [*Pseudotsuga menziesii* (Mirbel) Franco], white fir [*Abies concolor* (Gordon & Glendinning) Hoopes]), and limber pine (*Pinus flexilis* James) at the higher elevations and pinyon–juniper (*Pinus edulis* Engelm. and *Juniperus* spp.) woodland at the lower elevations (Allen 1989; USDI BAER Team 1996; Veenhuis 2002).

Soils in both study areas were derived from Bandelier Tuff, a volcanic parent material (Smith *et al*. 1970; Nyhan *et al*. 1978). Two soil series dominated the study area: Frijoles series (pumice, cindery, mesic Mollic and Typic Eutroboralfs, Andic Ustochrepts, and Typic Ustorthents) and Nyjack loam series (deep, very cindery, mesic Mollic and Typic Eutroboralfs). The Nyjack series are sandy loams located on hills and mountains (USDA Forest Service 1991).

Los Alamos (35°53′ N, 106°18′ W, 2258 m elevation), the closest long-term weather station, has mean maximum monthly temperatures of 4.1°C in January and 26°C in July (period of record 1961–1990). The mean daily minimum temperature is −7.6°C in January and 13.1°C in July. Mean annual precipitation is 469 mm, with 55% (258 mm) falling between June and September (http://www.wrcc.dri.edu/cgi-bin/cliNORMtM.pl?nmlosa). Summer monsoons are usually of high intensity, short duration, and often localized. For the years when we measured our transects, total June through September precipitation was 346.7 mm in 1997 and 186.2 mm in 1998. Spring (January–May) of 1997 also was unusually wet with gentle, well-spaced precipitation of 191.6 mm compared to the mean of 128.5 mm.

As a component of the BAER effort associated with the Dome Fire, moderate- and high-burn intensity areas in SFNF were seeded with almost 430 kg (425 seeds/m^2) of an annual

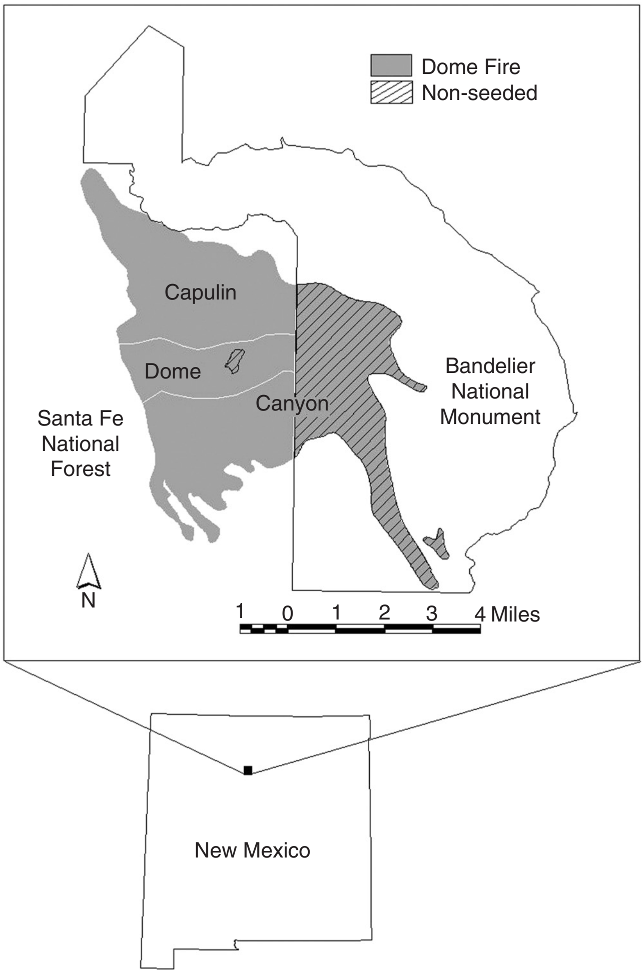

Fig. 1. Map of the study area showing different regions (Capulin, Dome, and Canyon), jurisdiction (Santa Fe National Forest *v.* Bandelier National Monument), and seeded *v.* non-seeded areas.

grass seed mix consisting of 23–30% ryegrass in mid-May, 1996 (Table 1). One area of moderate- and high-burn intensity was not seeded to serve as a control. BNM was not seeded after the fire. No data are available for the first growing season after the Dome Fire, except for a limited seed bank study in summer of 1996 (Snyderman 1996). The first significant rainfall occurred in mid-June, and by 15 July over 85% of the aerially applied seed either had been washed out of Snyderman's (1996) plots by surface runoff, failed to germinate or, if the seed germinated, the seedlings did not survive to 15 July. This figure increased to over 97% by 2 August. At the time of the 2 August sampling, there were more new non-graminoids (i.e. forbs and shrubs) in seeded than non-seeded areas, and approximately the same numbers of resprouting non-graminoids between seeded and non-seeded areas (Snyderman 1996). This seed bank study may not have been representative of the overall seeding success because there was considerable ryegrass establishment across many portions of the seeded burn area by September 1996.

Table 1. Percentage pure seed used after 1996 Dome Fire

From Agri Seed Testing Inc. (1996). Values do not add up to 100% because the remaining 22.11% and 17.77% was composed largely of inert matter (i.e. stems, chaff, empty florets, soil and broken seed) and, to a lesser extent, other crop seed and weed seed

	Mix (% of total)	
Pure seed components	1. Low elevation	2. Ponderosa pine/ High elevation
Lolium multiflorum	29.19	23.02
Bromus marginatus/carinatus		27.06
Elymus trachycaulus (Agropyron trachycaulum)	20.29	19.02
Bouteloua curtipendula	17.13	7.09
Schizachyrium scoparium	5.81	5.66
Oryzopsis hymenoides	4.90	
Dalea purpurea	0.57	0.38

Methods

Sampling and analysis

We initiated our study in the spring of 1997 to evaluate the post-fire and post-seeding recovery of vegetation. Study sites were classified into three strata based on combinations of burn intensity (unburned to low, moderate, or high), seeding treatment (seeded or non-seeded), and geographic area (Capulin, Dome, and Canyon). Burn intensity ranged from high (all needles in canopy consumed), to moderate (most needles in canopy scorched), to low and unburned (majority of needles in canopy remained green). Seeding treatments consisted of seeded (seeded with ryegrass mixture) (Table 1) or non-seeded (not seeded post-fire) (Fig. 1); application of seed was not under the control of this study. BNM (Canyon region) and one area in the SFNF (Dome region) were not seeded (Fig. 1). The three regions were defined according to elevation and location relative to average summer storm tracks over the Jemez Mountains. Geographically, Capulin was furthest to the north, Dome was most central, and Canyon was southernmost and includes both SFNF and BNM (Fig. 1). These regions were separated primarily to ensure adequate dispersion of transects across areas with different local climatic conditions, due to precipitation, aspect, and elevation, which might influence vegetation recovery. All study areas had slopes of 0–16° and were dominated by ponderosa pine prior to the fire. Soils in these areas were predominantly cindery or gravelly loams and a few were stony. None of the soils are particularly erodible.

In summer 1997, one 50-m transect was established at each of 49 randomly chosen points (across all treatments), oriented to follow the contour of the slope. The transects were unevenly distributed across the burn intensities: only seven transects were located in unburned sites (around the periphery of the Dome Fire), whereas 22 transects were located in the moderate burn intensity areas, and 20 transects were located in high burn intensity areas. If there is any bias in our sampling it is with the unburned sites, which included two of our lowest elevation transects. We recognize that spatial clustering of transects could introduce unintended bias into our analyses. A common native seed source, for example, might make closer transects more similar than distant ones. If such a spatial bias exists in our sampling, it would be with the moderate and high-intensity burned plots in the unseeded, control area.

The 0-m and 50-m ends of each transect were marked permanently with 61-cm aluminum stakes imprinted with transect name. Vegetation was measured at each transect once in 1997 and again in 1998 between the months of June and September. The line-intercept method (Canfield 1941; Mueller-Dombois and Ellenberg 1974) was used to measure cover of herbaceous vegetation. Foliar and basal cover of all live and dead vegetation (to the nearest cm) was measured as it intercepted the vertical plane above each transect. For each transect, we calculated (1) cover of ryegrass, (2) cover, species richness, and Shannon-Weaver Diversity Index ($e^{H'}$) for native forbs, and (3) cover of exotic vegetation minus ryegrass cover on each transect. The Shannon-Weaver Diversity Index ($e^{H'}$) represents the number of species that would be present if all species were equally abundant; it is a more intuitive metric than H′ (Magurran 1988; McPherson and DeStefano 2003). It was calculated by:

$$e^{H'} = e^{-\Sigma p_i \ln p_i},$$

where $p_i = N_i$ (% foliar cover of the *i*th species)/N (total % foliar cover of native forbs).

In 20 × 50-m plots centered on each transect, all conifer seedlings (e.g. ponderosa pine, limber pine, Douglas fir, white fir, and pinyon pine) (<1 m) were counted and identified to species when possible. Regeneration (number of conifer seedlings/plot in 1997) and survivorship of new conifer seedlings from 1997 to 1998 in each plot was estimated by:

$$\text{Survivorship} = \frac{(S_2 \text{ in } 1998) - (S_2 \text{ in } 1997)}{(S_1 \text{ in } 1997)} \times 100\%,$$

where S_1 and S_2 represent the number of 1-year and 2-year seedlings, respectively. Each seedling was aged as a first (<1 year old: S_1) or a second (≥ 1 year old: S_2) year seedling. Additionally, presence/absence of live adult conifers were noted in and around each plot. The corners of each plot were marked permanently with blank 61-cm aluminum stakes.

Conditions for regression models

We used multiple linear regression analysis with indicator variables using JMP® software (Sall *et al.* 2001) to examine the influence of treatments (e.g. seeding with ryegrass and burn intensity), year, and site effects [e.g. region, elevation, and Topographic Position Moisture Index (TPMI)] and their interactions (treatment × region, treatment × year, burn intensity × region) on ryegrass (foliar cover, basal cover), native forbs (foliar cover, basal cover, species richness, and diversity), conifer seedlings (regeneration, survivorship), and exotics (foliar cover, horseweed foliar [*Conyza canadensis* (L.) Cronq.] cover) (see Table 2). The raw data used were log/logit transformed in cases where they were not normally distributed: $\log(x+1)$ for species richness and diversity of native forbs and for the number of seedlings per plot; $\text{logit}(x+0.01)$ for values of ryegrass cover, native forb cover, conifer survivorship, exotic cover, and horseweed cover. TPMI is scaled from 0 (driest) to 50 (wettest), and is a relative estimate of site moisture status calculated from aspect, slope, and position on slope (Allen 1989, pp. 50–51, modified from Parker 1980).

Sample sizes were adjusted depending on the completeness of treatment and strata in the factorial structure of the multiple regression analysis. For example, because ryegrass was established only in ‘seeded’ areas, we excluded ‘seeded’ and ‘ryegrass cover’ treatments from models assessing the responses of ryegrass cover, and then fit a model including all three burn intensities, all three regions, elevation, TPMI, and year ($n = 98$) (Table 2). Because seeding treatment was not applied at all levels of each stratum (e.g. there were no moderate- or high-burn intensity areas that were not seeded in the Capulin region, and no unburned to low-burn intensity areas were seeded), we first examined subsets of data where the factorial structure of treatment and strata was complete. For example, for analyses of native forbs and exotics, we excluded the Capulin region and unburned to low-burn intensity areas from analyses ($n = 68$) (Table 2) to determine if trends in the complete subset paralleled those from the entire dataset. We omitted ‘year’ from the analysis of regeneration and survivorship of conifer seedlings ($n = 49$) because regeneration pertained only to 1997, and survivorship only to 1998. We examined similar subsets (excluding Capulin region and unburned to low-burn intensities) for regeneration ($n = 34$) (Table 2) of conifer seedlings. Survivorship of conifer seedlings was computed for plots in which regeneration was ≥ 1 seedling per plot in 1997 ($n = 37$). The sample size was reduced further by excluding the Capulin region ($n = 26$) (Table 2). In all instances, however, all data were presented in the graphs (Figs 2, 3, 4, 5 and 6). Because regeneration was examined in 1997 and survivorship in 1998, we also explored the influence of ryegrass cover in 1997 or 1998 on conifer seedlings. Cover of ryegrass in 1997 had greater influence, so it was used in the analyses of regeneration and survivorship of conifer seedlings. We also assumed that seeding treatment did not necessarily reflect the success of ryegrass establishment. Hence, we used either seeding treatment or ryegrass cover, whichever one had the lowest *P*-value, to assess the effect of seeding treatment on native forbs, conifer seedlings, and exotics.

Table 2. Influence (*P*-values) of treatments, site effects, year, and their interactions on ryegrass, native forbs, conifer seedlings, and exotics

Results are from multiple linear regression models

Response variable	*n*	Treatments			Site effects			Time	Interactions			Whole model results		
		Ryegrass cover	Seeding treatment	Burn intensity	Region	Elevation (m)	TPMI	(year)	Seeding treatment × region[D]	Seeding treatment × year[D]	Burn intensity × region[D]	*F*	d.f.	*P*
Ryegrass[A]	98													
Foliar cover				0.0016	0.10	0.0013	0.65	0.0001				6.69	7,90	<0.0001
Basal cover				0.14	0.30	0.06	0.73	0.46				1.48	7,90	0.18
Native forbs[B]	68													
Foliar cover		<0.0001		0.73	<0.0001	0.30	0.25	0.001	0.0005			15.19	7,60	<0.0001
Basal cover			0.28	0.45	<0.0001	0.42	0.01	0.0009	0.0041	0.05		5.71	8,59	<0.0001
Species richness		<0.0001		0.11	<0.0001	0.002	0.51	0.79	0.0032	0.032	0.0012	5.76	9,58	<0.0001
Diversity ($e^{H'}$)		<0.0001		0.42	0.0001	0.04	0.04	0.05	0.002		0.0054	4.18	8,59	0.0005
Conifer seedlings[B]														
Regeneration[C]	34	0.08[C]		<0.0001	0.31	0.01	0.23					13.34	5,28	<0.0001
Survivorship[C]	26	0.0008[C]		0.12	0.31	0.01	0.04					2.43	6,19	0.06
Exotics[B]	68													
Foliar cover		<0.0001		0.33	0.69	0.74	0.62	<0.0001		<0.0001		13.43	7,60	<0.0001
Horseweed Foliar cover			0.25	0.02	0.76	0.37	0.45	<0.0001		0.0002		12.50	7,60	<0.0001

[A] Ryegrass cover and seeding treatment were not included in models for cover of ryegrass.

[B] Ryegrass cover or seeding treatment, whichever one had the lowest *P*-value, was included in each model.

[C] Foliar cover of ryegrass in 1997. (See Methods, 'Conditions for regression models', paragraph 2.)

[D] Interactions presented only when significant.

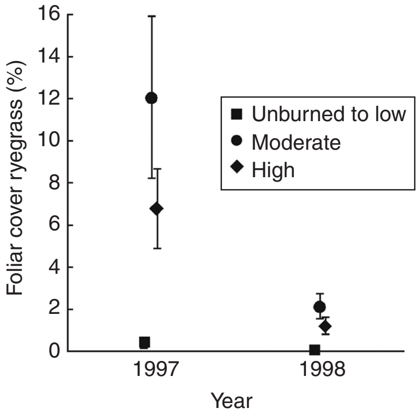

Fig. 2. Mean change in foliar cover of ryegrass from 1997 to 1998 across burn intensities. Vertical bars denote s.d. at 1 σ.

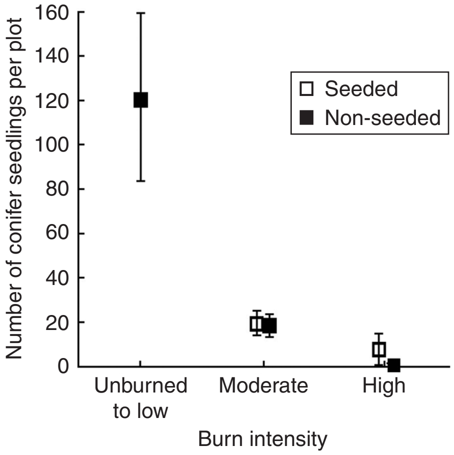

Fig. 3. Influence of burn intensity and seeding treatment on mean regeneration of conifer seedlings. Vertical bars denote s.d. at 1 σ.

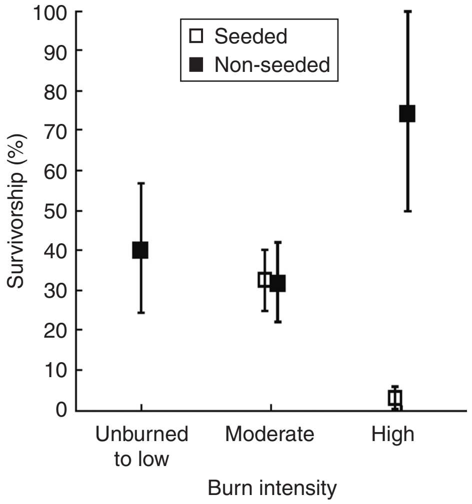

Fig. 4. Influence of burn intensity and seeding treatment on mean survivorship of conifer seedlings from 1997 to 1998. Vertical bars denote s.d. at 1 σ.

Results and discussion

Ryegrass cover

Foliar cover of ryegrass was greatest where it had been seeded in moderate-burn intensities (Fig. 2), after taking into account both elevation and year of sampling (Table 2). Ryegrass foliar and basal cover both increased with elevation. Foliar cover decreased (Fig. 2), but basal cover did not change, from 1997 to 1998 (Table 2). The decline of ryegrass foliar cover supports other research suggesting ryegrass may cause self-interference (McKell *et al*. 1969; Biswell 1974; Papanastasis 1976; Dodge 1979; Wakimoto 1979). Ryegrass quickly usurps nitrogen that is readily available after fire and sequesters it in mulch; it may actually deprive itself of nitrogen over the short term, explaining its quick exit from seeded areas in 3–5 years. Foliar cover may have been greater after the Dome Fire in areas of moderate- than high-burn intensities (Table 2; Fig. 2) because nitrogen was more available in less-intensely burned areas. Ryegrass also may have allelopathic properties (Cubbon 1925; Osvald 1949). Ryegrass produces toxic root exudates and water-soluble toxins in the above-ground portions of the plant in the laboratory; these toxins and exudates in the mulch chemically inhibit regeneration of new ryegrass individuals (Naqvi 1969). Other field studies, however, found no active inhibitors in ryegrass (Bowmer and McCully 1968).

Despite abundant seed crops, ryegrass has been shown to decline where temperatures are high and germination substrates consist of ryegrass litter (Young *et al*. 1975). This hinders establishment because seedlings are susceptible to drying and have virtually no root regeneration. Others have purported that ryegrass does not persist following a drought (Terry Johnson, personal communication 1998) or due to a combination of decreased nitrogen and low available soil moisture (Penny Leuhring, personal communication 1998). Therefore, the higher than average amount of rainfall in summer 1997 provided excellent growing conditions for ryegrass, but the average precipitation in 1998, in combination with decreasing available nitrogen, may have been inadequate. Finally, ryegrass is vulnerable to frost damage (Hunt 1962), which also may preclude its persistence in the high-elevation and frost-susceptible forests of the western USA.

Native forbs

Our evidence suggests that the multiplicative effects of seeding treatment × region influenced native forbs (Table 2). Foliar cover, basal cover, species richness, and diversity in seeded *v.* non-seeded areas in the Dome regions were similar, but values were much higher in non-seeded (BNM) than seeded (SFNF) areas in the Canyon region (Table 3). We attribute these differences to: (1) there was little non-seeded area in SFNF (one small interfluve with little topographic

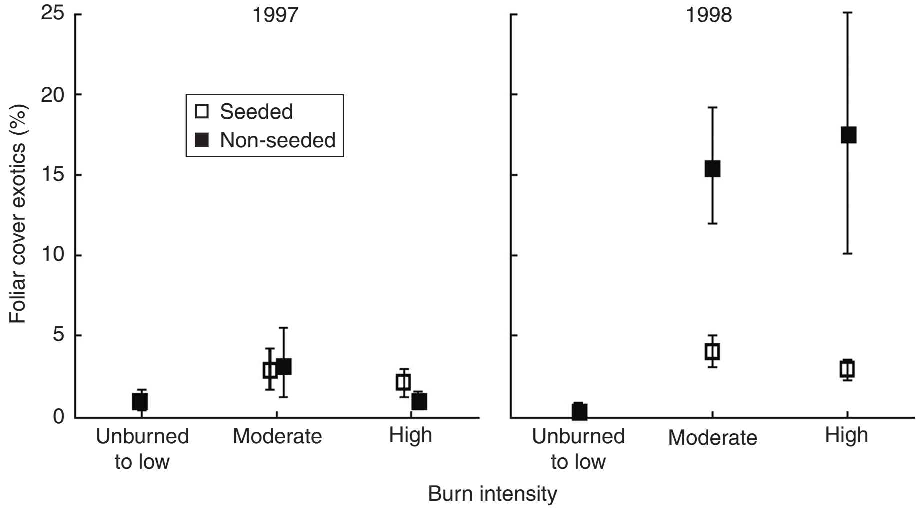

Fig. 5. Influence of year, burn intensity and seeding treatment on mean foliar cover of exotic plants. Vertical bars denote s.d. at 1 σ.

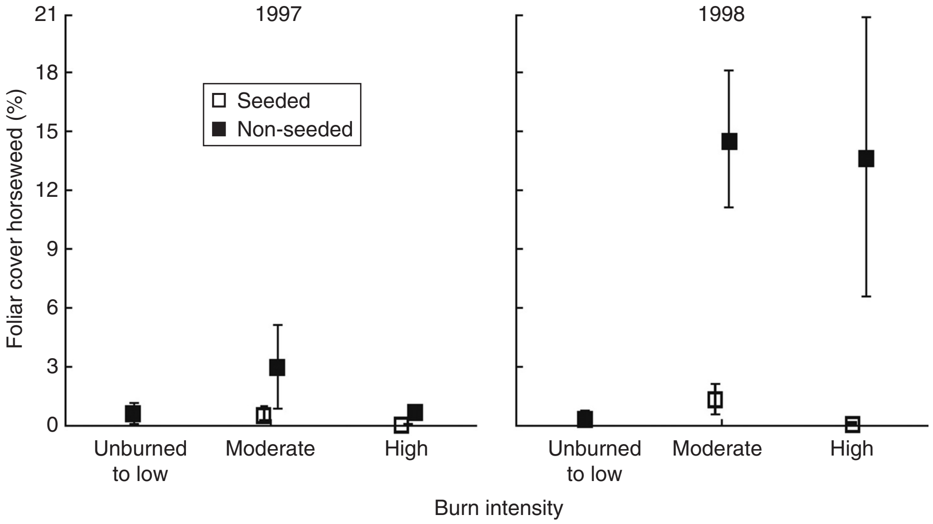

Fig. 6. Influence of year, burn intensity, and seeding treatment on mean foliar of horseweed. Vertical bars denote s.d. at 1 σ.

diversity), whereas all of BNM was non-seeded (more topographic and pre-fire vegetative diversity); (2) the non-seeded BNM transects are generally lower in elevation, and diversity tends to increase at lower elevations.

Foliar cover of native forbs decreased from 1997 to 1998 (Tables 2 and 3), as did five of the six most common native forbs. This might be explained by higher than average amount of rainfall in 1997 and less than average rainfall in 1998. The basal cover of native forbs also was influenced by the multiplicative effects of seeding treatment × year (Table 2). Cover in seeded areas did not change from 1997 to 1998, but cover in non-seeded areas did increase from 1997 to 1998 (Table 3). Perennial forbs may have been more successful in persisting in non-seeded areas, and they may have been better established in 1998 than 1997, resulting in larger plant bases (and increased basal cover) in 1998. Based on the values of foliar cover in 1997 and 1998, however, basal cover probably was underestimated in 1997, especially in seeded areas. Basal cover probably was estimated more accurately in 1998 and in the non-seeded areas; in 1998 there was less foliar cover of tall grasses such as ryegrass, and more native bunchgrasses and other native vegetation, which facilitated sampling.

Decreased basal cover of native forbs was associated with increased TPMI values (Table 2). If basal cover was estimated

Table 3. Responses of native forbs according to region, burn intensity, year, and seeding treatment

Region	Burn intensity	Year	Foliar cover (%)						Basal cover (%)						Species richness						Diversity ($e^{H'}$)					
			Seeded			Non-seeded			Seeded			Non-seeded			Seeded			Non-seeded			Seeded			Non-seeded		
			n	$\bar{x}$	s.e.	*n*	$\bar{x}$	s.e.	*n*	$\bar{x}$	s.e.	*n*	$\bar{x}$	s.e.	*n*	$\bar{x}$	s.e.	*n*	$\bar{x}$	s.e.	*n*	$\bar{x}$	s.e.	*n*	$\bar{x}$	s.e.
Capulin	High	1997	4	8.57	3.03	–	–	–	4	0.015	0.015	–	–	–	4	4.0	0.7	–	–	–	4	2.77	0.53	–	–	–
		1998	4	1.36	1.00	–	–	–	4	0.050	0.033	–	–	–	4	2.5	1.3	–	–	–	4	1.82	0.75	–	–	–
	Moderate	1997	4	11.94	5.69	–	–	–	4	0.020	0.008	–	–	–	4	7.0	1.2	–	–	–	4	3.44	0.99	–	–	–
		1998	4	5.50	2.51	–	–	–	4	0.240	0.100	–	–	–	4	5.5	1.5	–	–	–	4	2.36	0.76	–	–	–
	Unburned to low	1997	–	–	–	2	10.09	0.13	–	–	–	2	0.050	0.050	–	–	–	2	12.0	4.0	–	–	–	2	4.68	2.28
		1998	–	–	–	2	6.50	1.64	–	–	–	2	0.330	0.270	–	–	–	2	10.0	4.0	–	–	–	2	3.42	1.63
Dome	High	1997	4	2.17	1.03	4	3.71	3.33	4	0.025	0.025	4	0	0	4	3.5	1.3	4	2.8	0.8	4	2.11	0.52	4	1.74	0.10
		1998	4	1.22	0.86	4	1.07	0.35	4	0.020	0.016	4	0.040	0.023	4	3.0	1.1	4	3.5	0.5	4	2.21	0.58	4	0.31	0.46
	Moderate	1997	5	2.17	1.03	4	2.96	1.14	5	0.016	0.012	4	0.010	0.010	5	4.4	0.9	4	3.8	1.3	5	2.52	0.56	4	2.64	0.82
		1998	5	2.06	0.40	4	3.26	2.42	5	0.072	0.020	4	0.150	0.087	5	4.4	0.5	4	4.3	1.7	5	2.55	0.42	4	2.08	0.45
	Unburned to low	1997	–	–	–	2	3.82	0.68	–	–	–	2	0	0	–	–	–	2	7.0	0	–	–	–	2	3.05	1.26
		1998	–	–	–	2	3.61	0.17	–	–	–	2	0.080	0.080	–	–	–	2	6.5	2.5	–	–	–	2	2.88	0.65
Canyon	High	1997	4	16.74	8.56	4	37.49	8.76	4	0.200	0.120	4	0	0	4	8.3	3.2	4	8.8	1.3	4	2.80	1.18	4	3.70	0.68
		1998	4	7.22	6.01	4	24.00	8.80	4	0.090	0.083	4	0.570	0.240	4	6.0	2.1	4	8.8	1.9	4	3.38	0.95	4	3.46	1.44
	Moderate	1997	5	8.88	4.93	4	34.69	3.14	5	0	0	4	0.250	0.120	5	6.8	2.6	4	8.8	0.9	5	2.38	0.69	4	4.69	1.00
		1998	5	7.32	5.99	4	19.00	3.61	5	0.190	0.120	4	0.500	0.310	5	4.6	1.5	4	8.3	1.3	5	1.87	0.54	4	2.90	0.48
	Unburned to low	1997	–	–	–	3	11.64	0.17	–	–	–	3	0.020	0.020	–	–	–	3	9.3	1.9	–	–	–	3	2.99	0.81
		1998	–	–	–	3	9.08	1.75	–	–	–	3	0.230	0.120	–	–	–	3	6.3	1.2	–	–	–	3	2.31	0.40

accurately, however, it seems that increased site moisture (TPMI) resulted in decreased basal cover of native forbs because they prefer drier sites (Table 2). Alternatively, basal cover of native forbs may have been higher in drier sites because they were out-competed by grasses at wetter sites.

Species richness of native forbs was also influenced by the multiplicative effects of seeding treatment × year, as well as burn intensity × region (Table 2). In contrast to basal cover, species richness was the same in 1997 and 1998 in the non-seeded areas, but richness decreased from 1997 to 1998 in seeded areas (Table 3). This may mean that fewer species germinated and were established in 1998 than 1997 in seeded areas. Because there was no change in the non-seeded areas, it seems plausible to assume that the decrease in the seeded areas was influenced by seeding treatment (or ryegrass cover), and that this influence is persistent.

Species richness and diversity of native forbs also was influenced by the multiplicative effects of burn intensity × region (Table 2). It was similar in moderate-burn intensity areas in the Canyon and Dome regions, but richness was greater in high-burn intensity areas of the Canyon than those in the Dome region (Table 3). For reasons not well understood, richness and diversity were greater in areas of high-burn intensity in the Canyon *v.* the Dome region, whereas they did not differ between the two regions in areas of moderate burn intensity.

Species richness and diversity decreased as elevation increased (Table 2), so it appears that more native forb species in the Dome Fire study area inhabit lower than higher elevations. Diversity decreased from 1997 to 1998 (Table 3), similar to foliar cover of native forbs, presumably due to the higher than average amount of precipitation in 1997 and the average amount in 1998. Finally, increasing diversity was positively related to site moisture (TPMI) (Table 2).

Conifer seedlings

Regeneration of conifer seedlings decreased as foliar cover of ryegrass increased in 1997, after accounting for burn intensity and elevation. Mean survivorship of conifer seedlings also decreased (from 1997 to 1998) as foliar cover of ryegrass in 1997 increased, after accounting for elevation and TPMI (Table 2). The presence of ryegrass in 1997 negatively impacted conifer regeneration and survivorship potentially through competition for water, nutrients, space, and light, or from allelopathic effects. Similar results were obtained in the Santa Lucia Mountains, Monterey County, California (Griffin 1982), where conifer seedlings had higher survivorship in non-seeded than seeded plots, and in the Sierra Nevada Mountains, where density of conifer seedlings decreased with increased ryegrass cover (Conard *et al*. 1991). In some seeded plots within the Dome Fire area, estimates of regeneration may be low, and estimates of survivorship may be high because ryegrass and other seeded grasses may have been too dense for all newly germinated conifer seedlings to be counted in 1997.

Mean regeneration and survivorship of conifer seedlings were influenced by burn intensity (Table 2), regeneration was lowest in high-burn intensity areas (Fig. 3), and survivorship was lowest in high-burn intensity areas that were seeded (Fig. 4). Distance from plot center to nearest live, adult conifer tree apparently influenced conifer regeneration. Plots that had no trees within 50 m of the center of the plot ($n = 15$) had an average of 0.8 (s.e. ± 0.4) conifer seedlings per plot. Those plots that had at least one live, adult conifer within 50 m of the center of the plot ($n = 7$) or within the plot ($n = 27$) had 3.1 (s.e. ± 1.4) and 49.2 (s.e. ± 13.0) conifer seedlings per plot, respectively. Distance from plot center to nearest live, adult conifer tree was associated with burn intensity ($R^2 = 0.47$). Even if a seed is dispersed into a high-burn intensity, seeded area and germinates, it is very unlikely (3.2%) that it will survive even to the next year. This is primarily due to the seeding treatment because survivorship of conifer seedlings was highest (75%) in high-burn intensity, non-seeded areas (Fig. 4). Hence, the bare soil requirement for germination of ponderosa pines probably was met in all three areas of burn intensities, but only the unburned to low- and moderate-burn intensity areas met the seed-source requirement due to the proximity and density of standing live trees that persisted post-fire.

Regeneration increased with increasing elevation to 2500 m, and survivorship was related positively to elevation (Table 2). The two transects at the highest elevations (2518 and 2591 m) had no conifer seedling regeneration, but they were both in high-burn intensity areas that were seeded. Survivorship was related positively to TPMI, so conifer seedlings evidently were more likely to survive to the second year where moisture levels are high.

Exotic species

Foliar cover of exotic species (not including ryegrass) depended on the multiplicative interaction of seeding treatment × year (Table 2; Fig. 5). Exotic cover increased in response to moderate- and high-burn intensities, and thrived in the non-seeded areas, especially in 1998. Interestingly, the majority of cover in non-seeded areas in 1998 can be attributed to horseweed, an annual, cool- or warm-season, exotic forb in the Asteraceae family that is common in wastelands throughout North America. This species competes intensely for water, grows quickly (http://www.ipm.ucdavis.edu/PMG/WEEDS/horseweed.html), and can rapidly become a problem under a no-tillage condition (http://www.nal.usda.gov/ttic/tektran/data/000007/07/0000070735.html). The horseweed fruit is a 1–1.5-mm long achene with many small white bristles that aid in wind dispersal. This dispersal mechanism apparently aided this species in colonizing these moderate- and high-burn intensity areas lacking vegetation cover from adjacent seeded areas. Although horseweed responds opportunistically to disturbances like fire, it is not aggressively persistent; i.e. from visual inspection, its populations are much reduced in the transects 6 years after the Dome Fire (Craig Allen, personal observation in summer 2003).

Cover of exotic species was similar in seeded and non-seeded areas in 1997, but increased in non-seeded areas from 1997 to 1998, and did not change from 1997 to 1998 in seeded areas (Fig. 5). Horseweed was also affected by the multiplicative interaction between treatment × year, and was largely responsible for the upsurge in exotic cover in non-seeded areas from 1997 to 1998 (Table 2; Fig. 6). Horseweed cover also was influenced by burn intensity (Table 2); it was highest in moderate-burn intensities (Fig. 6).

Conclusions

Post-seeding studies should span 5 or more years, or incorporate rainfall simulations, to account for the strong influence of climate variability on seeding success, post-fire erosion, and the nature and rates of native vegetation recovery. Inferences from the Dome Fire study are limited in scope due to timing (sampling should have started in the growing season immediately following seeding), sampling strategies and application of treatments (need for greater randomization), and a lack of replication in time and space (more sites over a greater number of years should be measured).

Proponents of ryegrass seeding argue that ryegrass does not threaten the long-term functionality of ecosystems (i.e. interfere with native species) because it tends to leave the system within 3–5 years. Even the short-term presence of ryegrass, however, may attenuate the long-term succession of native, successional forbs. The Dome Fire study suggests that ryegrass cover (or seeding treatment), in combination with region or year (i.e. time since seeding or annual precipitation), reduced space and resources otherwise available to native forbs. Ryegrass may prevent the establishment of post-fire seeders, or at least may preclude them from producing a viable seed reserve before the next fire (Griffin 1982). A limited seed bank study conducted in the summer immediately following the Dome Fire suggests that there were actually higher densities of new non-graminoids (e.g. forbs and shrubs) in seeded than non-seeded areas in 1996 (Snyderman 1996). By 1997 and 1998, however, cover, species richness, and diversity of native forbs actually were lower in seeded than non-seeded areas. Ryegrass suppression of native forb production and diversity could in fact have persistent effects on post-fire vegetation recovery.

There are other drawbacks to seeding with ryegrass. First, seeding augments fine fuels prone to rapid rates of fire spread, and increases the chances for early reburns (Schultz and Biswell 1952; Nadkarni and Odion 1986). Early reburns are unnatural and kill regenerating shrub and tree seedlings (Griffin 1982; Zedler *et al*. 1983). In high-burn intensity areas with few surviving trees, forest regeneration could be forestalled by a lack of available seed if a reburn occurs within a decade of the initial fire. We found that seeds rarely come from trees more than 50 m away, so the impact may be significantly magnified with increasing area of reburn. In addition, early reburns can destroy root biomass and increase erosion potential (Nadkarni and Odion 1986). Ryegrass also attracts gophers, and burrowing may increase soil movement and subsequent erosion (Taskey *et al*. 1989).

Studies examining the success of ryegrass seeding on curbing erosion have been inconclusive or have shown mixed results. Even if ryegrass stems erosion in the first few years, the expense of seeding and risk of introducing non-native forbs and grasses may not be worth the delayed succession of native plant communities. The Cerro Grande Fire, which burned 19 283 ha in the Jemez Mountains in 2000, required one of the largest BAER efforts ever in the USA. Extensive seeding with ryegrass, a major component of the 360 000 kg of grass seed applied in the first year after the Cerro Grande Fire (http://web.em.doe.gov/tie/fire.html), inadvertently introduced over 1 billion cheat-grass (*Bromus tectorum* L.) seeds as contaminants to the burn area (unpublished data reported to Cerro Grande Fire BAER team). This resulted in increased establishment and prevalence of cheatgrass across the burned area.

In the near future, seeding and other post-fire rehabilitation methods will be considered indispensable as wildfire severity increases with the present glut in fuels and the many obstacles to fuel treatment (Allen *et al*. 2002), the prospects for continuing drought (Gray *et al*. 2003), and the growing risks to watersheds in this semi-arid region (Moody and Martin 2001). In particular, massive rehabilitation efforts after severe fire years (e.g. summer 2002 Rodeo-Chedisky Fire and summer 2003 Aspen Fire in Arizona) highlight the need for continued post-seeding studies in ponderosa pine forests of the south-western USA. Future studies should address issues of seed banks, ryegrass suppression of native forbs and conifer seedlings, effectiveness of ryegrass in curbing soil erosion and reasons why ryegrass tends to exit the system 3–5 years from seeding.

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