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Minimal effectiveness of native and non-native seeding following three high-severity wildfires

Ken A. Stella[A,C], *Carolyn H. Sieg*[B] *and Pete Z. Fulé*[A]

[A]School of Forestry and Ecological Restoration Institute, Northern Arizona University, PO Box 15018, Flagstaff, AZ 86011, USA.
[B]USDA Forest Service, Rocky Mountain Research Station, 2500 South Pine Knoll Drive, Flagstaff, AZ 86001, USA.
[C]Corresponding author. Email: kstella@fs.fed.us

Abstract. The rationale for seeding following high-severity wildfires is to enhance plant cover and reduce bare ground, thus decreasing the potential for soil erosion and non-native plant invasion. However, experimental tests of the effectiveness of seeding in meeting these objectives in forests are lacking. We conducted three experimental studies of the effectiveness of seeding with non-native and native species following three Arizona wildfires. Seeding treatments were largely ineffective in increasing vegetative cover or decreasing exposed bare ground. At one treatment at one fire, wheat seeding at the Warm Fire, senesced seeded annuals increased litter cover and resulted in lower bare ground values than unseeded controls. Only on one fire, the Warm Fire, did seeded non-native annuals establish well, resulting in 20–29% vegetative cover. On the other two fires, seeded cereal grains accounted for $<3\%$ cover. At all fires, native seeded species contributed between <1 and $\sim 12\%$ vegetative cover. Vegetative cover on all treatments, including unseeded treatments, was at or near 40% the first year following fire, at all three study sites. Non-native species richness and abundance did not differ among treatments at any fire. This study adds to growing evidence that post-fire seeding is ineffective in enhancing post-fire plant cover and reducing invasive non-native plants.

Additional keywords: annual ryegrass, Burned Area Emergency Rehabilitation, exotic plants, fire rehabilitation, ponderosa pine, wheat.

Introduction

High-severity wildfires in forested ecosystems consume high percentages of aboveground biomass, vegetative cover, litter and duff (Ryan and Noste 1985). The increase in bare mineral soil, light and nutrient availability following high-severity wildfires may increase water runoff and soil erosion, and facilitate non-native plant invasions (Benavides-Solorio and MacDonald 2001; Crawford *et al.* 2001; Johansen *et al.* 2001). In an attempt to ameliorate the effects of high-severity wildfires, resource managers frequently apply post-wildfire treatments, such as contour felling of logs, mulching and seeding. Owing to its low cost, ease of application, and long history of use, seeding is the most widely applied post-wildfire treatment (Beyers 2004). Species used in post-wildfire seeding are most commonly quick-growing non-native grasses (Robichaud *et al.* 2000). Quick growth is important because the risk of increased runoff and erosion is highest in the first year after fire (Robichaud *et al.* 2006; Wagenbrenner *et al.* 2006). Seeded species most commonly utilised include non-native cereal grains, which are either sterile hybrids or annuals with low reproductive potential in forested ecosystems (Robichaud *et al.* 2000). Seeding with longer-lived native perennial species has been recommended to produce more persistent vegetative cover and standing crop compared with seeding with annuals (Richards *et al.* 1998; Beschta *et al.* 2004). However, use of native seeded species in post-wildfire rehabilitation has been limited and there is relatively little published information on the effectiveness of native species in meeting post-fire vegetative cover objectives (Beschta *et al.* 2004).

Post-wildfire seeding is predicated on the assumption that seeding will enhance plant cover and reduce bare ground, thereby reducing runoff and erosion rates (Robichaud *et al.* 2000; Beyers 2004). Conceptually, the relationship between cover and reduced erosion is two-fold. First, plant cover prevents rainsplash and sheet erosion by intercepting precipitation before it strikes the soil surface (DeBano *et al.* 1998). Second, plant roots increase soil water infiltration and can aid in the deterioration of hydrophobic soil layers that may result from high-severity wildfires (Benavides-Solorio and MacDonald 2001).

The proportion of exposed bare ground and ground covered are important predictors of post-fire runoff and erosion rates. Several studies from forested ecosystems have demonstrated significant positive correlations between the percentage of exposed bare ground and both water runoff and soil erosion (Benavides-Solorio and MacDonald 2001; Johansen *et al.* 2001). These studies have shown consistent significant increases in soil loss as exposed soil reaches >60–70% on severely burned areas (Johansen *et al.* 2001). Other research has shown a negative correlation between ground cover

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compared with post-fire water runoff and soil erosion (Johansen *et al.* 2001; Wagenbrenner *et al.* 2006). Post-fire erosion studies from coniferous forests support the concept that high vegetative cover results in low amounts of runoff and erosion rates (Johansen *et al.* 2001; Wagenbrenner *et al.* 2006). Recent studies from coniferous forests including ponderosa pine (*Pinus ponderosa* C. Lawson) and grand fir (*Abies grandis* Douglas ex D. Don) have demonstrated that a minimum of 50–70% cover is most closely associated with low amounts of runoff and erosion (Johansen *et al.* 2001; Robichaud *et al.* 2006; Wagenbrenner *et al.* 2006). Researchers and land managers commonly use 60% cover as a target value in evaluating the effectiveness of seeding treatments (Robichaud *et al.* 2000; Beyers 2004; Keeley 2004; USDA Forest Service 2004).

Preventing or reducing the abundance of invasive non-native species after fire is often a goal of seeding (Robichaud *et al.* 2000; Beyers 2004). The assumption is that seeded species will grow quickly and utilise available resources, thus co-opting them from invading non-natives. Previous research suggests the degree to which non-native abundance is reduced depends on the resulting dominance of the seeded species in the post-fire plant community. Studies from wildfires and prescribed burns have shown seeding, whether with native or non-native species, had little effect on non-native species abundance owing to low dominance of seeded species (Kruse *et al.* 2004; Springer and Laughlin 2004; Daniels *et al.* 2008; Kuenzi *et al.* 2008). In contrast, two studies demonstrated short-term reductions in non-native species following post-wildfire seeding with either wheat (Keeley 2004) or native seed mixes (Thompson *et al.* 2006); in both cases, seeded species had high dominance in the post-fire plant community.

Experimental tests of the effectiveness of post-wildfire seeding of native and non-native species in enhancing plant cover and standing crop, reducing bare ground, and curtailing invasive non-native plants are rare. Thompson *et al.* (2006), who experimented with native and non-native seeding in a sagebrush (*Artemisia* spp.) steppe plant community, is a notable exception, but we were unable to find similar studies from coniferous forests. Most studies have been opportunistic and observational, in that researchers have established study areas within large landscape-level seeding treatments implemented by managers following fire. This has led to difficulty in locating unseeded control areas for comparisons as well as uncertainty over the amount of seed applied at the plot level of observation (Schoennagel and Waller 1999; Barclay *et al.* 2004; Kruse *et al.* 2004). The result of these difficulties can be small sample sizes and weak inferences.

We took advantage of three separate, high-severity wildfires that occurred in ponderosa pine forests. We used a controlled, replicated and randomised experimental design to determine the effects and effectiveness of native and non-native seeding in the first year following fire. We hypothesised that seeding would: (1) decrease bare ground; (2) increase plant canopy cover and standing crop; and (3) reduce non-native species abundance and richness.

Methods

Study areas

We selected three wildfires in Arizona ponderosa pine forests (Fig. 1). The Potato and Warm Fires burned in 2006; the Birdie Fire burned in 2007. We sampled immediately post burn and 1 year after fire, the period within which plant establishment is required to meet rehabilitation objectives. Replicated, randomised, controlled experimental plots were established in areas dominated by ponderosa pine, within 4 weeks of fire containment, on high-severity portions of the burn, as defined by federal Burned Area Emergency Rehabilitation (BAER) teams. Severity classification was ground-truthed by visually assessing tree mortality, crown scorch height, and ground char (Ryan and Noste 1985).

The fires spanned an elevational gradient (Fig. 1). The Warm Fire burned from 8 June to 4 July 2006 on the Kaibab National Forest. This fire had the highest average elevation, 2400 m, and the greatest average yearly precipitation, 64.5 cm (Western Regional Climate Center, see www.wrcc.dri.edu, accessed 6 June 2009); soils were predominantly Mollic Eutroboralfs with a sandy loam texture derived from limestone parent materials (Brewer *et al.* 1991). The Potato Fire burned 6–28 June 2006 on the Apache–Sitgreaves National Forest. This fire had the lowest average elevation, 2050 m, and the lowest average yearly precipitation, 52.4 cm (www.wrcc.dri.edu). The dominant soil types were Lithic and Typic Eutroboralfs; these moderately deep gravelly soils with a sandy loam texture were derived from basaltic parent materials (Laing *et al.* 1991). The Birdie Fire burned 6–15 July 2007 on the Coconino National Forest. The average elevation, 2200 m, and average annual precipitation, 59 cm, are intermediate relative to those at the Warm and Potato Fires (Miller *et al.* 1991; www.wrcc.dri.edu). The dominant soil type was Mollic Eutroboralfs with cobbly loam texture derived from basaltic parent materials (Miller *et al.* 1991). Precipitation at all three sites approximated long-term averages in the year of fire and the first year following fire (Fig. 2). Fire containment, plot establishment, and seeding all occurred within 1 to 3 weeks of the onset of high-intensity summer monsoonal precipitation (Fig. 2; www.wrcc.dri.edu).

Experimental design and treatments

We established fifteen 20×25-m (500-m^2) plots per treatment at each fire. Plots were located within unseeded areas of high-severity burn, with slopes between 5 and 25%. The minimum distance between plots was 100 m, and plots were randomly located with respect to aspect, soil type, and prefire conifer abundance. Data were collected immediately and 1 year post fire. Experimental treatments randomly assigned to plots were: (1) seeding with non-native common wheat (*Triticum aestivum* L.); (2) seeding with non-native annual ryegrass (*Lolium multiflorum* Lam.); (3) seeding with a native seed mix including: squirreltail (*Elymus elymoides* (Raf.) Swezey), blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths), muttongrass (*Poa fendleriana* (Steud.) Vasey), scarlet gilia (*Ipomopsis aggregata* (Pursh) V.E. Grant), and purple locoweed (*Oxytropis lambertii* Pursh.); plus (4) unseeded control. Owing to fire size, treatments varied between fires. At the Potato and Birdie Fires, treatments 1, 3 and 4 were tested; at the Warm Fire, all four treatments were tested. Our target seeding rate was 403 pure live seeds (PLS) m^{-2} (Table 1), based on the USDA Natural Resources Conservation Service (2004) recommended rate of 269 PLS m^{-2} with an increase of 1.5 to 2 times for broadcast seeding. These seeding rates are similar to those used

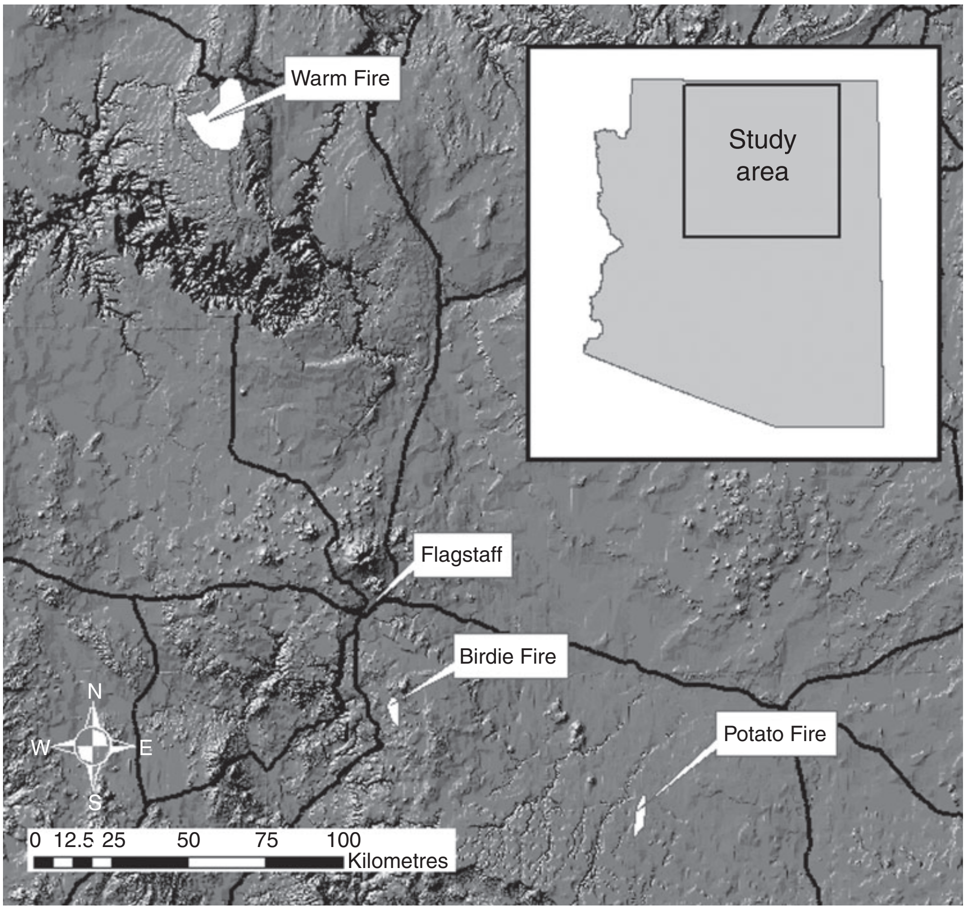

Fig. 1. Location of study sites. Warm Fire, 23 702 ha; Birdie Fire, 2180 ha; and Potato Fire, 7200 ha.

in other post-fire seeding experiments (Robichaud *et al.* 2000; Thompson *et al.* 2006). Seed was hand broadcast at each plot immediately following plot establishment.

Species used in seed treatments were selected because they are commonly used by land managers or showed promising results in studies in this region (Jones 1998; Robichaud *et al.* 2000; Elseroad *et al.* 2003; Barclay *et al.* 2004). Annual ryegrass was seeded on portions of the Warm Fire and the 1997 Dome Fire in New Mexico (Barclay *et al.* 2004). Wheat was seeded on portions of the Potato Fire and the 2002 Rodeo–Chediski Fire in Arizona (Kuenzi *et al.* 2008). We included species with broad geographic distributions and included both cool-season (C3: bottlebrush squirreltail, muttongrass, and purple locoweed) and warm-season (C4: blue grama and scarlet gilia) plants in an effort to enhance plant cover throughout the growing season (Dodge 2004; Springer and Laughlin 2004; Moore *et al.* 2006; Daniels *et al.* 2008).

Response variables

We estimated each of the following variables: total live plant canopy cover, litter, rock, and bare ground cover, plus cover by life form (graminoids, shrubs, and forbs) and by species in fifty 20×50-cm (0.1-m^2) quadrats per plot. We placed the quadrats at 1-m intervals on the right side of five permanent transects in each plot. We estimated cover by classes ($1 = <1\%$, $2 =$ 1–5%, $3 = 6$–25%, $4 = 26$–50%, $5 = 51$–75%, $6 = 76$–95%, $7 = 96$–100%) modified from Daubenmire (1959). We added the $<1\%$ class based on Bailey and Poulton's (1968) recommendation to better describe vegetation occurring in very small amounts. We used midpoints of each cover class to calculate averages.

Plant standing crop was sampled in each plot by clipping herbaceous vegetation in fifteen 0.25-m^2 circular quadrats, three per transect, randomly placed along the left side of each transect. Clipped material was separated by species in the field, placed in paper bags, oven-dried for 48 h at 70°C, and weighed to the nearest 0.01 g (Moore *et al.* 2006).

We sampled between the end of July and the end of August to capture plant cover and biomass present at the onset of high intensity monsoonal rainstorms (www.wrcc.dri.edu). These rainstorms account for approximately half of yearly precipitation in this region (www.wrcc.dri.edu). Plant nomenclature and nativity are according to the Plants Database (http://plants.usda.gov, accessed 6 March 2009). Plant reference specimens are stored at the Ecological Restoration Institute at Northern Arizona University, Flagstaff, Arizona.

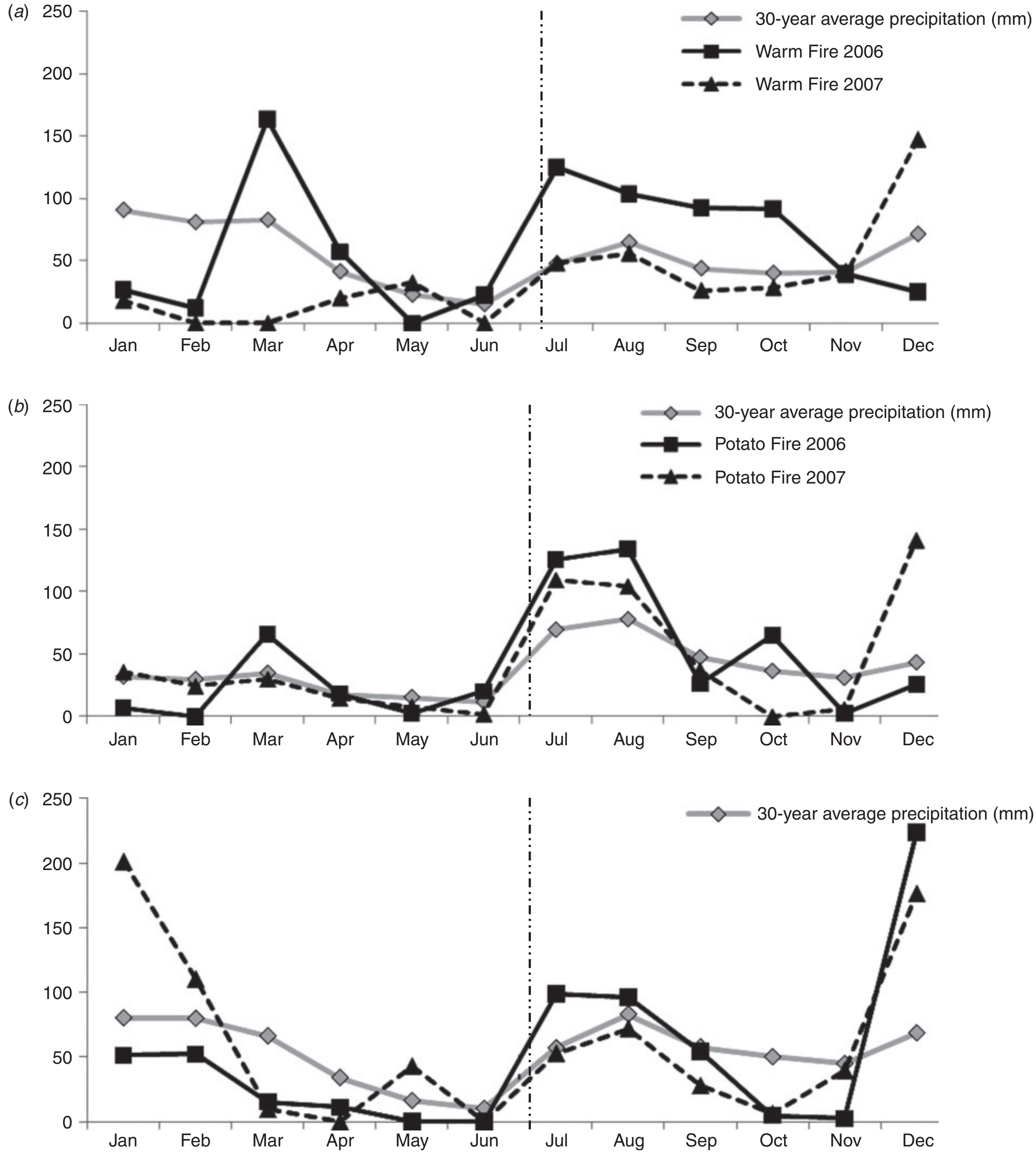

Fig. 2. Thirty-year average precipitation and precipitation for study sites during sampling years. Vertical dashed line is the approximate date of fire containment and date of application of seeding treatments. (*a*) Warm Fire; (*b*) Potato Fire; (*c*) Birdie Fire.

Statistical analysis

Owing to differences in site characteristics, dates of burn, and variations in treatments applied, we analysed each fire as a separate experiment. We tested assumptions of normal distribution of data using the Shapiro–Wilk test and homogeneous variances using the Levene test in *JMP* ver. 7.0.1 (SAS Institute Inc. 2009). Owing to non-normality and heterogeneous variances in many of our response variables, we used non-parametric testing procedures (Anderson 2001).

We used PERMANOVA analysis in *PC-ORD* ver. 5.1 with Bray–Curtis distance measures for all analyses, although similar results were observed using Euclidean distances (Faith *et al.* 1987; Ludwig and Reynolds 1988; McCune and Mefford 1999). PERMANOVA is a distance-based non-parametric analysis of

Table 1. Seeding treatment species, average pure live seeds (PLS) per kilogram, target application rates (seeds m^{-2}), and percentage of species in seed mixes

No.	Treatment type	Species	Target application rate (seeds m^{-2})	Percentage of mix	Seed origin
1	Annual ryegrass	*Lolium multiflorum*	403	100%	Field-grown, Utah
2	Common wheat	*Triticum aestivum*	403	100%	Field-grown, Idaho
3	Native species	Native seed mix	403 combined		
		Elymus elymoides	173	43%	Field-grown, Washington
		Bouteloua gracilis	80	19.8%	Collected, Colorado Plateau
		Poa fendleriana	50	12.4%	Collected, Colorado
		Ipomopsis aggregata	50	12.4%	Collected, Colorado Plateau
		Oxytropis lambertii	50	12.4%	Collected, Colorado Plateau
4	Unseeded	None	0		

variance procedure that can be used with univariate or multivariate datasets. We used 9999 permutations per test (Anderson 2001). When significant differences were detected among treatments, we used a non-parametric pair-wise *a posteriori* *t*-test to separate means (Anderson 2001). For all tests, we used $\alpha = 0.05$ to determine significance.

We tested for differences among treatments immediately post fire and 1 year following fire. Immediately post fire, but before seeding treatments were applied, we tested for differences in substrate, litter, and plant cover among treatments. At 1 year following fire, we tested for differences among treatments in total plant cover, standing crop and cover of non-native species (excluding seeded non-natives), litter and bare ground. We also analysed cover and standing crop by life-form (graminoids, forbs, shrubs) by treatments.

Results

Does seeding decrease bare ground?

Immediately post-fire, before treatments were applied, bare ground ranged from 42 to 48% at the Warm Fire, 65 to 68% at the Potato Fire, and 55 to 60% at the Birdie Fire (all standard errors (s.e.) $< 5.2\%$). There were no significant differences in bare ground among treatments at the Potato, Birdie or Warm Fires ($P = 0.86$, 0.89, 0.76 respectively). Immediately post fire, litter cover ranged from 19 to 39% across all treatments at all three fires; rock cover ranged from 5 to 13% and log cover averaged $< 1\%$. There were no significant differences in litter, rock or log cover among treatments at the Potato, Birdie or Warm Fires (litter: $P = 0.69$, 0.99, 0.69; rock: 0.95, 0.99, 0.50; log: 0.96, 0.76, 0.95 respectively). Residual post-fire vegetative cover averaged between < 0.5 and 5.0%, with no significant difference among treatments at any fire.

In the first year after seeding, bare ground did not differ among treatments at the Potato ($P = 0.99$) or Birdie Fires ($P = 0.77$) (Fig. 3*a*). Bare ground differed among treatments only at the Warm Fire, with significantly ($P = 0.03$) lower levels on plots seeded with wheat than unseeded treatments (Fig. 3*a*). This difference was explained by higher levels of litter at the Warm Fire wheat treatments compared with the unseeded treatments ($P = 0.02$), 52% cover of litter at the wheat treatments compared with 36% on unseeded treatments, with native treatments and ryegrass treatments having intermediate amounts (42 and 47% respectively). Litter cover did not differ among treatments at the Potato, where litter cover ranged from 25 to 27% ($P = 0.91$) or Birdie Fires, where litter cover ranged from 59 to 61% ($P = 0.88$).

Does seeding increase ground cover, plant cover, and standing crop?

Warm Fire

Total canopy cover was significantly higher on ryegrass seeded plots ($P < 0.01$) and native seeded plots ($P = 0.04$) compared with unseeded plots (Fig. 3*b*). The total canopy cover was ~13% higher on the ryegrass treatments and ~10% higher on native seeded treatments compared with unseeded controls. Wheat treatments produced an intermediate amount of cover ~9% greater than unseeded controls, which did not differ significantly from unseeded controls. However, total plant standing crop did not differ among treatments ($P = 0.28$) (Fig. 4*a*).

Seeding altered the abundance of graminoids. Graminoid cover and standing crop differed significantly ($P = 0.02$ and < 0.01) among treatments, with higher graminoid cover and standing crop on seeded plots compared with unseeded controls. Annual ryegrass and wheat were major species in terms of canopy cover on their respective treatments (Table 2*a*). On the native seed treatment, two seeded grasses, squirreltail and muttongrass, dominated plant cover and standing crop. Major species on unseeded plots included squirreltail, muttongrass, a native *Carex*, and a variety of native forbs. Graminoid standing crop on unseeded controls was the lowest at 54.4 kg ha^{-1} (s.e. 12.5) compared with the native seeded treatment at 114.2 kg ha^{-1} (s.e. 21.2), the ryegrass at 163 kg ha^{-1} (s.e. 36.1), and the wheat treatment had the highest at 368.8 kg ha^{-1} (s.e. 97.2). Total forb cover, standing crop and shrub cover did not differ significantly among treatments ($P = 0.51$, 0.29 and 0.12) (Fig. 4*a*).

Potato Fire

Total plant canopy cover ($P = 0.43$) and plant standing crop ($P = 0.33$) did not differ significantly among treatments in the first year following fire (Figs 3*b*, 4*b*). Similarly, we did not detect significant differences in canopy cover ($P = 0.33$) or standing crop ($P = 0.48$) of graminoids among treatments (Fig. 4*b*). Nor was there a significant difference in total forb cover ($P = 0.51$) or standing crop ($P = 0.36$) among treatments. There were only trace amounts of shrub species.

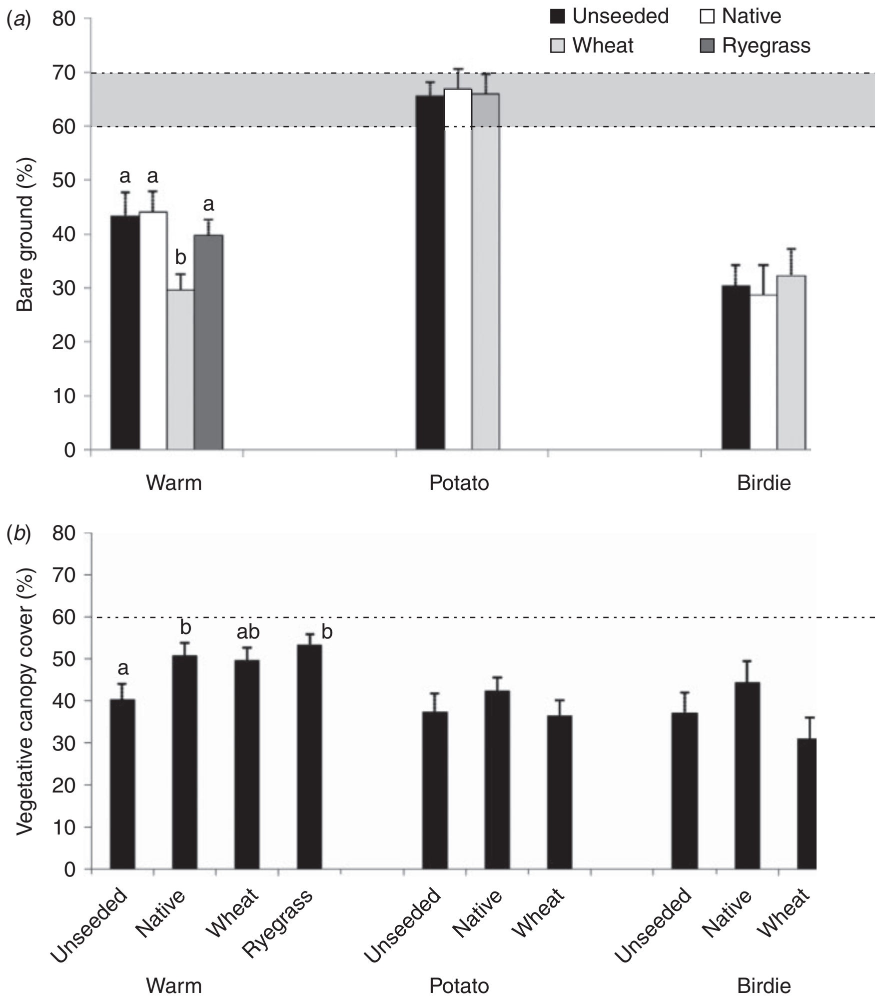

Fig. 3. (*a*) Bare ground first year following fire; area between dashed lines is range of bare ground values above which runoff and erosion significantly increase (Johansen *et al.* 2001). (*b*) Total canopy cover in the first year following fire, dashed line is target cover value associated with lower risk of increased erosion and runoff (Robichaud *et al.* 2000). Different letters above means indicate significant differences among treatments when they were detected.

In contrast to the Warm Fire, species included in the seed mixes were not always the major species in terms of plant canopy cover. Wheat cover at the Potato Fire averaged $<2\%$ on the wheat seed treatment, and on the native seed treatment, only two seeded species, blue grama and squirreltail, had cover $>2\%$ (Table 2*b*). Instead, native forbs originating from natural regeneration and recruitment dominated plant canopy cover on all treatments the first year following burning.

Birdie Fire

Total vegetative cover ($P = 0.31$) and standing crop ($P = 0.74$) did not differ among treatments in the first year following fire (Figs 3*b*, 4*c*). However, graminoid cover and standing crop differed among treatments ($P = 0.03$ and 0.01), with higher levels on native seeded treatments compared with both unseeded and wheat treatments. Graminoid standing crop on unseeded controls was 105.9 kg ha^{-1} (s.e. 22.9) compared with 173.2 kg ha^{-1} (s.e. 20.3) on the native seeded treatment, and 75.8 kg ha^{-1} (s.e. 21.3) on the wheat treatment (Fig. 4*c*).

The Birdie Fire was similar to the Potato Fire in that wheat had very low cover in the first year following fire (~2%) (Table 2*c*). On the native seeding treatment, two seeded species, blue grama and squirreltail, were major species. On unseeded plots, native forbs and graminoids constituted the majority of the post-fire plant cover. Shrub cover ranged from 1.5 (s.e. 0.5) to 4.6% (s.e. 1.8) on the three treatments.

Does seeding reduce non-native species?

Plant standing crop of non-native species (excluding seeded species) was highly variable and did not differ among treatments at any fire (Potato fire: $P = 0.17$, Birdie Fire: $P = 0.82$; we detected only trace amounts of non-natives at the Warm Fire). Non-native species richness (other than the seeded species) ranged from 4 to 11 species on the three fires and did not differ among treatments on any fire ($P > 0.77$).

In the first year post burn at the Warm Fire, we found five non-native species: cheatgrass (*Bromus tectorum* L.), bull thistle (*Cirsium vulgare* (Savi) Ten.), redstem stork's bill (*Erodium*

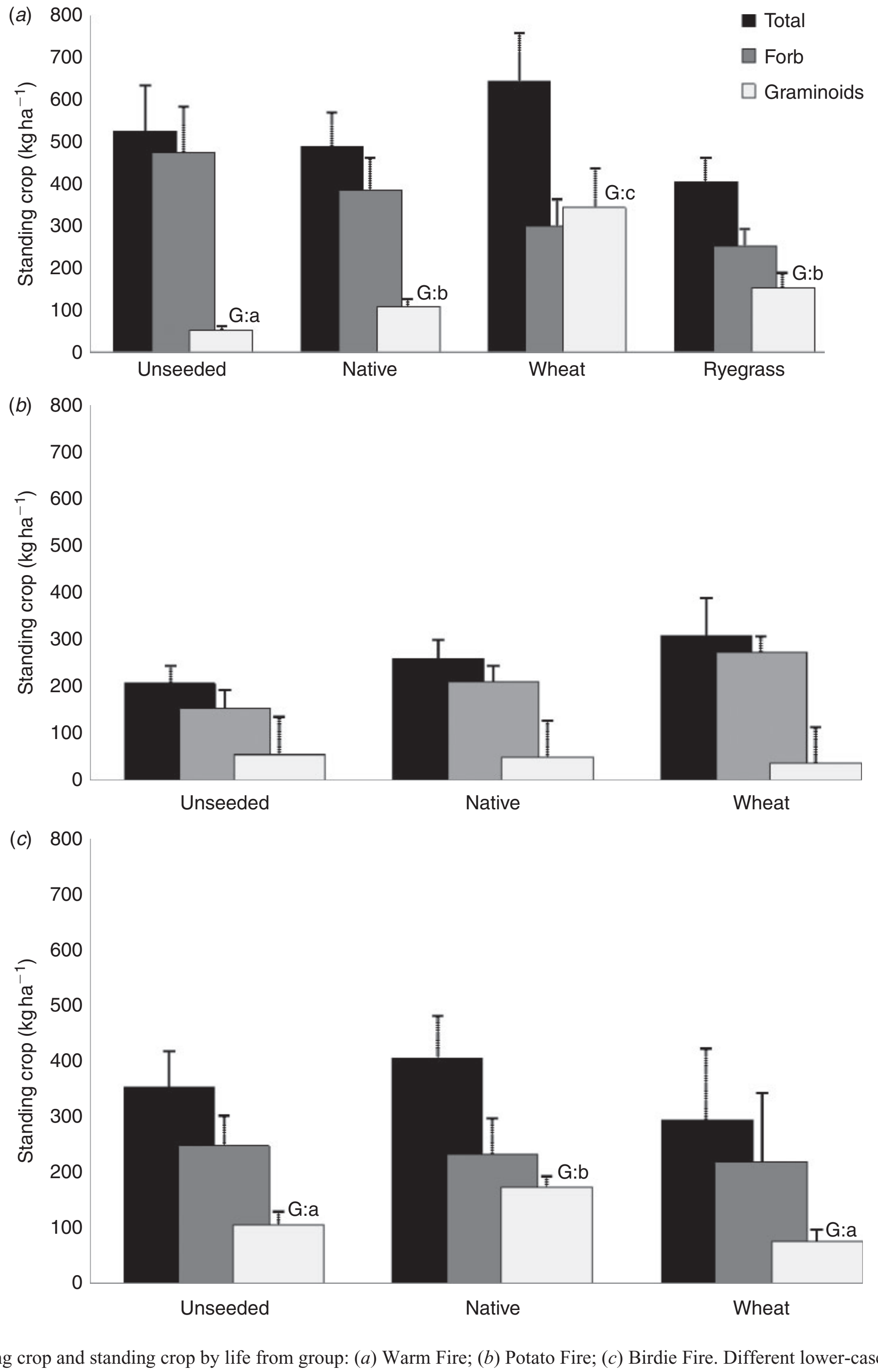

Fig. 4. Total standing crop and standing crop by life from group: (*a*) Warm Fire; (*b*) Potato Fire; (*c*) Birdie Fire. Different lower-case letters above means indicate significant differences among treatments; upper case letters note life-form groups (G = graminoids).

cicutarium (L.) L'Her. Ex Aiton), common dandelion (*Taraxacum officinale* F.H. Wigg.) and yellow salsify (*Tragopogon dubius* Scop.). Richness of non-natives among treatments was similar, with the exception of yellow salsify, which was not present on the native seeded treatments.

Non-native species at the Potato Fire in the first year following fire were bull thistle, redstem stork's bill, little hogweed (*Portulaca oleracea* L.) and common mullein (*Verbascum thapsus* L.). Little hogweed was prevalent on all plots but owing to its diminutive stature, accounted for little standing crop. Bull

Table 2. Average (standard error) percentage plant canopy cover of graminoids and forbs, plus cover of seeded species by treatment in the first year post burn

t, <0.5% cover; †, non-native species. (*a*) Warm Fire; (*b*) Potato Fire; (*c*) Birdie Fire

Species	Treatment			
	Unseeded	Native	Wheat	Ryegrass
(*a*) Mean plant canopy cover (%) seeded species, Warm Fire				
Total graminoid cover	12.79 (1.7)	23.97 (2.43)	27.11 (3.5)	33.29 (3.92)
Bouteloua gracilis	0.79 (0.39)	0.88 (0.22)	0.65 (0.35)	0.38 (0.22)
Elymus elymoides	3.15 (1.29)	11.64 (2.32)	1.75 (0.58)	0.92 (0.25)
Poa fendleriana	4.73 (0.96)	7.66 (1.78)	3.71 (0.99)	5.18 (1.16)
Lolium multiflorum†				29.06 (3.47)
Triticum aestivum†			20.71 (3.38)	
Total forb cover	27.07 (3.58)	29.51 (3.14)	23.09 (2.84)	22.49 (2.7)
Ipomopsis aggregata	t	3.14 (0.13)	t	t
Oxytropis lambertii	t	0.7 (0.05)	t	t
(*b*) Mean plant canopy cover (%) seeded species, Potato Fire				
Total graminoid cover	12.04 (2.53)	13.5 (1.51)	8.58 (1.43)	
Bouteloua gracilis	1.19 (0.92)	2.84 (0.74)	0.68 (0.30)	
Elymus elymoides	0.13 (0.09)	2.89 (2.32)	0.04 (0.25)	
Poa fendleriana	0.45 (0.19)	0.15 (0.05)	0.25 (0.18)	
Triticum aestivum†			1.75 (0.25)	
Total forb cover	27.4 (2.75)	31.67 (2.84)	29.5 (3.25)	
Ipomopsis aggregata	t	1.15 (0.94)	t	
Oxytropis lambertii	t	0.5 (0.05)	t	
(*c*) Mean plant canopy cover (%) seeded species, Birdie Fire				
Total graminoid cover	16.88 (3.39)	29.86 (4.89)	16.19 (3.55)	
Bouteloua gracilis	0.75 (0.46)	9.83 (2.37)	0.15 (0.11)	
Elymus elymoides	3.35 (1.71)	5.26 (1.64)	1.29 (0.80)	
Poa fendleriana	t	t	t	
Triticum aestivum†			2.06 (1.19)	
Total forb cover	23.04 (3.8)	16.71 (3.36)	15.49 (3.55)	
Ipomopsis aggregata	t	t	t	
Oxytropis lambertii	t	1.14 (0.34)	t	

thistle was absent from native seeded plots. All these species made up trace (<2% of total non-native standing crop) amounts, except mullein, which was responsible for the majority of the non-native standing crop. Distribution and abundance of mullein varied among treatments but not significantly owing to the large variation. Mullein occurred on one-third of the total plots and accounted for an average of between 7 and 30% of total standing crop (mullein standing crop: unseeded plots (12.7 kg ha^{-1}, s.e. 8.5), native (40.6 kg ha^{-1}, s.e. 30.8), and wheat plots (102 kg ha^{-1}, s.e. 68).

Eleven non-native species were present at the Birdie Fire (cheatgrass, bull thistle, prickly lettuce, prostrate knotweed (*Polygonum aviculare* L.), little hogweed, Canada bluegrass (*Poa compressa* L.), Kentucky bluegrass (*Poa pratensis* L.), Dalmatian toadflax (*Linaria dalmatica* L. Mill.), common dandelion, yellow salsify, and common mullein). Two species occurred only on native seeded plots (yellow salsify and Canada bluegrass). The two most abundant non-natives were Kentucky bluegrass and common mullein; together, they accounted for over 90% of non-native standing crop at all treatments. Similar to the Potato Fire, the distribution of these species varied greatly, occurring on less than one-third of the plots. When these species occurred, they accounted for between 21 and 40% (between 70.6 kg ha^{-1}, s.e. 31.1 and 152.2 kg ha^{-1}, s.e. 113.64) of total standing crop.

Discussion

Does seeding decrease bare ground?

Immediately post fire, the percentage of bare ground on two fires was above 55%, thus potentially putting these sites at risk for increased sediment loss. On the Warm Fire, bare ground was lower, but still within the range considered to be at risk for increased sediment yields following intense storms (Robichaud *et al.* 2000; Wagenbrenner *et al.* 2006). A year later, bare ground on all treatments at the Potato Fire changed little and remained at levels potentially at risk for increased erosion. The percentage of bare ground at the Birdie Fire, regardless of treatment, declined to levels low enough to curtail erosion (Johansen *et al.* 2001). At the Warm Fire, wheat seeding significantly decreased bare ground compared with all other treatments, largely owing to increased litter cover from the senesced wheat. Levels of bare ground at the Warm Fire on all treatments, including unseeded controls, were low enough to protect sites from all but the most intense storms (Johansen *et al.* 2001; Pannkuk and Robichaud 2003; Groen and Woods 2008). Thus, with the exception of wheat seeding on one fire, seeding treatments were largely ineffective in decreasing bare ground. At two fires, litter accumulations and plant regeneration on all treatments, including unseeded treatments, resulted in bare ground values well below those associated with increased runoff and erosion (Johansen *et al.* 2001).

The ineffectiveness of seeding treatments at reducing bare ground we documented is similar to several previous post-wildfire studies (Robichaud *et al.* 2006; Wagenbrenner *et al.* 2006). In fact, evidence supporting the effectiveness of seeding in significantly reducing bare ground is limited. Amaranthus *et al.* (1993) reported significant reductions in bare ground following seeding with annual ryegrass, and Keeley (2004) reported similar results with wheat seeding at high rates. In both of these studies, and in our one treatment where the proportion of bare ground was lower, the resulting reductions in bare ground were attributed to a thatch layer produced by the senesced seeded annuals.

Does seeding increase plant cover and standing crop?

Our results, along with previous research from both experimental and observational studies, indicate post-wildfire seeding treatments are largely ineffective in significantly increasing vegetative cover in forested ecosystems in the first year following fire (Robichaud *et al.* 2000) (Table 3). Where we did find differences in cover resulting from seeding, the unseeded treatments averaged 40% cover, whereas the native treatments averaged 49%, and the ryegrass averaged 53% cover. However, whether these differences in vegetative cover will confer substantial reductions in post-fire runoff and erosion is unclear (Benavides-Solorio and MacDonald 2001; Johansen *et al.* 2001). Using the target cover value of 60%, no treatment achieved this level of cover in the first year following fire (Robichaud *et al.* 2000; Johansen *et al.* 2001).

Although seeding is predicated on the assumption that plant regeneration following high-severity fire will be slow and seeding will increase cover, we found relatively high amounts of vegetative cover on all unseeded treatments in all three case studies (Robichaud *et al.* 2000). Plant species utilising multiple regeneration and recruitment strategies were present in the post-fire plant community. These included perennial plants regenerating from underground persistent root masses, regeneration of species that are known to produce persistent seed banks, and colonising species (Wienk *et al.* 2004; Korb *et al.* 2005; http://plants.usda.gov).

Standing crop sampling accounts for differences in plant architecture that were not captured in vegetative cover values; for example, annual ryegrass is relatively prostrate (high relative cover and low standing crop) whereas wheat has a vertical architecture (low relative cover and high standing crop). At one fire, increased graminoid standing crop was attributable to seeded annual species. Seeded annuals complete their lifecycle in one growing season, senesce, and in following growing seasons can contribute to increased litter but not to belowground biomass (Amaranthus *et al.* 1993; Schoennagel and Waller 1999; Keeley 2004). In contrast, increased graminoid standing crop associated with native seeded perennials will likely persist into subsequent years, contributing to belowground biomass (Gill *et al.* 2002). Seeding native perennial species has been promoted as an alternative to annuals to encourage longer-term ecosystem rehabilitation (Richards *et al.* 1998; Beschta *et al.* 2004). As the risk of soil erosion following fire is the greatest in the first few growing seasons, a successful treatment would need to produce high amounts of standing crop quickly following treatment application (Wagenbrenner *et al.* 2006). Neither native nor non-native seeding treatments resulted in higher total standing crop in the first year.

The minimal effectiveness of seeding in increasing vegetative cover or standing crop that we found may be linked to timing and intensity of precipitation (Robichaud *et al.* 2000). High-intensity rains can physically remove and transport surface materials including seeds (Johansen *et al.* 2001) and have been linked to low success of seeding in previous research (Robichaud *et al.* 2006; Wagenbrenner *et al.* 2006). In the mountainous western United States, such high-intensity rainstorms commonly coincide with or immediately follow mid-summer fires (Swetnam and Betancourt 1990). At all of our study sites, the onset of high-intensity summer rainstorms coincided with fire containment, plot establishment and seeding.

Another factor that may have limited the success of some of our seeded native species is the origin of the seed. Four of the five seeded species were from regionally local sources; however, the squirreltail that comprised almost half of the seed mix was from a non-local source. There is evidence, both at small and regional scales, that many species are genetically adapted to site-specific conditions (Grant 1982; Millar and Libby 1989; Raabova *et al.* 2007). The risk of seeding with native species that are not locally adapted is two-fold. First, the seed may be poorly adapted to site-specific conditions, and germination and success of seeding may be reduced (Raabova *et al.* 2007). Second, gene flow from introduced plants may swamp local populations, effectively removing or altering patterns of local adaptation (Jones 1998; McKay *et al.* 2005). The degree to which non-local genetics of native seeded species affected our results is unknown, but could have lasting consequences.

Does seeding reduce non-native species?

We attributed the ineffectiveness of seeding in altering the abundance or richness of non-native species in the first year to two factors. First, non-native abundance was relatively low on all three fires. Second, even the most successful seeding treatment resulted in inadequate plant cover to exclude non-natives (Grace 1999; Grime 2001). Species exclusions are generally associated with high cover or dominance of seeded species in the plant community (Barclay *et al.* 2004; Keeley 2004). At our two fires where non-natives occurred in higher than trace amounts, seeded wheat established $<3\%$ cover and seeded native perennial species provided between 4 and 14% cover. Thus, seeded species abundance was too low to influence non-native abundance. Thompson *et al.* (2006) found lower non-native annuals on plots seeded with native perennials in the third growing season post burn, indicating the potential longer-term benefits of seeding with native perennial species.

Seeding to control non-native species following a high-severity wildfire is often based on the assumption that non-natives will increase following fire; however, this may not always be the case. Recent studies show two distinctly different patterns regarding non-native species invasions following high-severity fires in ponderosa pine forests. The first pattern indicates colonising species, including non-natives, increase following high-severity fire (Crawford *et al.* 2001; Griffis *et al.* 2001; Hunter *et al.* 2006). In contrast, the second pattern

Table 3. Total plant cover on seeded and unseeded treatments and plant cover of seeded species in the first year following high-severity wildfires

The first nine studies were originally reported in Robichaud *et al.* (2000) and last seven studies were either not published in the original review or published since the original review. Cover values are treatment averages if given, otherwise ranges (low–high) are shown; 'n.d.' is shown when no data were provided. Statistical difference between treatments, when reported, is signified by an asterisk

Study location	Vegetation type	Treatment type	Seeded species cover/total cover	Unseeded control cover (%)	Source
Siskiyou Mountains, OR	Douglas-fir	Annual ryegrass	49/50*	9	Amaranthus (1989)
Siskiyou Mountains, OR	Douglas-fir	Annual ryegrass	85.2/87.1*	23.6	Amaranthus (1989)
Near Loman, ID	Douglas-fir	Non-native mix	1/14	15	Geier-Hayes (1997)
Near Loman, ID	Ponderosa pine	Non-native mix	3/10	n.d.	Geier-Hayes (1997)
Near Loman, ID	Subalpine fir	Non-native mix	n.d./7	n.d.	Geier-Hayes (1997)
Near Greenville, CA	Mixed conifer	Native–non-native mix	n.d./6	7	Roby (1989)
Entiat Experimental Forest, WA	Ponderosa pine–Douglas-fir	Non-native mix	3.3/10.3	5.6	Tiedemann and Klock (1973)
Snow Basin, OR	Pine–mixed fir	Non-native mix	12/44*	12	Anderson and Brooks (1975)
Santa Lucia Mountains, CA	Sugar pine	Annual ryegrass	5 to 70/10 to 75	5	Griffin (1982)
Pocatello, ID	Sagebrush–juniper–grassland	Non-native mix	n.d./12.8	18.3	Ratzlaff and Anderson (1995)
Eastern Cascades, WA	Grand fir	Native–non-native mix	n.d./41.5	48	Schoennagel and Waller (1999)
North-western CA (Megram Fire)	Mixed-conifer	Barley + mulch	n.d./31.1	24.3	Kruse *et al.* (2004)
Jemez Mtns, NM	Ponderosa pine	Annual ryegrass	n.d./16.7	37.5	Barclay *et al.* (2004)
Central Sierras, CA (Highway Fire)	Mixed ponderosa pine–oak	Common wheat	67/95*	55	Keeley (2004)
North-central WA (North 25 Fire)	Mixed-conifer	Common wheat	4.5/18	18	Robichaud *et al.* (2006)
Tintic Valley, UT	Pinyon juniper	Native–non-native mix	4/4.3	7	Thompson *et al.* (2006)

indicates non-natives do not increase following fire (Huisinga *et al.* 2005; Kuenzi *et al.* 2008). Huisinga *et al.* (2005) attributed low non-native species abundance in a National Park to low propagule pressure due to low levels of anthropogenic influence. However, our three study sites and those of Kuenzi *et al.* (2008) have a long history of active management and resource utilisation, and both of these studies documented low levels of non-native species following high-severity wildfires.

Some research has indicated the risk of non-native species invasion following high-severity disturbances may increase over time (Keeley 2004). If this is true for semiarid ponderosa pine forests, seeding with ephemeral non-native cereal grains or sterile hybrid species would not be effective in reducing invasions in future growing seasons, as timing of the greatest abundance of seeded species would not coincide with non-native species increases. Some researchers have demonstrated longer-lived perennial species may reduce the abundance of non-native species in the third growing season and beyond (Thompson *et al.* 2006), implying seeding with native perennials may be a more appropriate method of curtailing non-native species invasions. However, studies examining non-native species abundances in the second or third year following high-severity wildfires in ponderosa pine forests do not demonstrate increases in these plants (Huisinga *et al.* 2005; Kuenzi *et al.* 2008).

Although the abundance and richness of non-natives is, so far, low on our study sites, some non-native species present are considered 'transformer' species and may increase, or have negative ecological effects, over time (Richardson *et al.* 2000). Of the 11 non-native species we recorded, six are listed as noxious in at least one south-western state (University of Montana Invaders Database, http://invader.dbs.umt.edu/, accessed January 2010; http://plants.usda.gov): cheatgrass, bull thistle, redstem stork's bill, Dalmatian toadflax, little hogweed and common mullein. Some of these species can significantly alter ecosystem structure or function in other forested systems (D'Antonio and Vitousek 1992; Oliff *et al.* 2001; D'Antonio *et al.* 2004). Longer-term monitoring of these sites is warranted to both assess population trajectories of these non-native species and to better evaluate the relative effectiveness of seeding treatments in restoring native plant communities.

Conclusion

The efficacy of post-wildfire seeding to increase vegetative cover, reduce bare ground, and prevent non-native species invasion following fire is not well supported by previous research (Robichaud *et al.* 2000). When seeding has resulted in high levels of vegetative cover the first post-fire growing season, it has been in more mesic conifer ecosystems (Amaranthus 1989) or when seed was applied at high rates (Keeley 2004). In drier ecosystems, including chaparral and ponderosa pine forests, seeding has been ineffective in producing high levels of vegetative cover (Beyers 2004; Wagenbrenner *et al.* 2006). Additionally, natural regeneration resulting from increased light and nutrient availability often yields high levels of vegetative cover without seeding following fire (Keeley *et al.* 2003; Huisinga *et al.* 2005). Here, we provide evidence for low vegetative cover and standing crop from seeding in ponderosa pine forests using a replicated experimental design on three wildfires with both native and non-native seeding treatments.

Seeding has been shown to have negative effects on plant communities, which may have long-term negative effects on plant regeneration. Beyers' (2004) review noted that in the cases when seeding provided cover values thought to significantly reduce erosion, there were negative ecological effects as a result of the high abundance of seeded species. Some of these negative effects included reduced abundance of conifer, shrub and annual colonising species (Schoennagel and Waller 1999; Keeley 2004). This pattern of dominant species reducing abundance of other species in plant communities is well documented (Stohlgren *et al.* 2003; Smith *et al.* 2004; Spehn *et al.* 2004), and in this context is counter to long-term goals of ecosystem rehabilitation (Keeley 2004). Thus, the paradox of seeding following fires is that seeded species need to produce high amounts of cover to effectively reduce bare ground and non-native species invasions, but high cover and dominance of seeded species is often associated with negative impacts to plant community regeneration (Beyers 2004; Keeley 2004).

The high financial cost and low potential for effectiveness should call into question the continued practice of seeding areas burned in high-severity wildfires. Robichaud *et al.* (2000) estimated that post-wildfire rehabilitation over the last decade cost US$48 million and Wolfson *et al.* (2005) reported US$6 million was spent in Arizona and New Mexico over a 2-year period. Both of these reviews indicate that seeding was the most widely applied post-wildfire treatment. Our study adds to the growing evidence that post-fire seeding is often ineffective in enhancing post-fire plant cover, reducing bare ground, or reducing invasive non-natives.

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