Understory responses to fire and artificial seeding in an eastern Cascades *Abies grandis* forest, U.S.A.[1]

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Abstract: To mitigate erosion after fire, land managers often seed non-native grasses onto burned slopes. To assess how post-fire seeding affects plant recovery, we compared areas that were either unseeded or artificially seeded after high-intensity fire in a dry *Abies grandis* (Dougl.) Lindl. forest in the northeastern Cascades. Seeding with a mix of non-native grasses and a legume significantly reduced the cover of native plants and shifted patterns of relative abundance after 2 years. Although seeding did not significantly affect total cover or native species richness, it reduced overall native plant cover by 47%. Species that recolonize via wind-dispersed seeds (e.g., *Epilobium angustifolium* L., *Lactuca serriola* L., and *Arenaria macrophylla* Hook.), species with long-lived seeds that germinate after fire (e.g., *Ceanothus velutinus* Dougl.), and species with wide successional amplitudes that resprout after fire (e.g., *Apocynum androsaemifolium* L. and *Salix scouleriana* Barratt) all declined steeply in cover on seeded plots. In addition, conifer seedlings were only half as abundant on seeded plots. As seeding after fire does not boost total plant cover and limits conifer tree establishment on the study area, it appears to do little to reduce the risk of soil erosion. It also appears to inhibit native shrub and herb re-establishment. These substantial effects on native species appear to alter plant communities well beyond the life of the seeded species.

Résumé : Pour réduire l'érosion après feu, les aménagistes du territoire sèment souvent des graminées exotiques sur les pentes brûlées. En vue d'établir comment l'ensemencement après feu affecte la reprise de la végétation, les auteurs ont comparé des aires non ensemencées avec des aires ensemencées artificiellement à la suite d'un feu de forte intensité, dans une forêt sèche d'*Abies grandis* (Dougl.) Lindl. des Cascades nord-orientales. Après 2 ans, l'ensemencement avec un mélange de graminées exotiques et d'une légumineuse a réduit, de façon significative, le couvert des plantes indigènes et a changé les patrons d'abondance relative. Bien que l'ensemencement n'ait pas affecté de façon significative le recouvrement total et la richesse des espèces indigènes, il a tout de même réduit le recouvrement général des plantes indigènes de 47%. Le recouvrement des espèces qui recolonisent les aires incendiées grâce à leurs semences anémochores (ex., *Epilobium angustifolium* L., *Lactuca serriola* L. et *Arenaria macrophylla* Hook.), celui des espèces dotées de semences d'une grande longévité qui germent après feu (ex., *Ceanothus velutinus* Dougl.) et celui des espèces possédant une grande amplitude successionnelle qui rejettent de souche après feu (ex., *Apocynum androsaemifolium* L. et *Salix scouleriana* Barratt) a fortement diminué dans les parcelles ensemencées. En plus, dans les parcelles ensemencées, l'abondance des semis de conifères a diminué de moitié. Étant donné que l'ensemencement après feu n'augmente pas le recouvrement total des plantes et qu'il limite l'établissement des arbres conifériens dans l'aire étudiée, il semble contribuer peu à la réduction du risque de l'érosion du sol. Il semble aussi inhiber la réinstallation des arbustes et des herbes indigènes. Ces effets substantiels sur les espèces indigènes altèrent probablement les communautés végétales bien au-delà de la survie des espèces ensemencées.

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Introduction

Fire plays key ecological roles in dry coniferous forests of the U.S. Inland West (Arno 1980; Pyne 1982; Wright and Bailey 1982; Kauffman 1990; Agee 1993; Johnson et al.

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1994, Langston 1995). Almost a century of active fire suppression and logging have altered the species composition and stand structure of low- to mid-elevation dry forests (Wischnofske and Anderson 1983; Camp et al. 1995; Arno et al. 1995, 1997) and apparently increased the occurrence of intense wildfire in areas historically dominated by frequent, low-intensity surface fires (Mutch et al. 1993).

As intense fires have increased across dry western forests, managers have struggled to adopt appropriate fuels-management techniques to reduce fire potential (Wilson and Dell 1971; Dodge 1972; Countryman 1974; Arno and Brown 1991). Forest managers have also attempted to reduce threats of soil erosion after major wildfires by seeding steep, intensively burned slopes (Anderson and Brooks 1975; Clary 1988; Conrad et al. 1989; Gross et al. 1989; Ruby 1989). In part, this seeding reflects managers' doubts that

native plants can quickly and adequately revegetate these areas (U.S. Department of Agriculture (USDA) 1978, 1990*b*, 1995). Non-native grasses are commonly chosen for post-fire seeding because they are low in cost and readily available. Such seeding with non-native grasses is increasingly used as an emergency method both to reduce threats of erosion and, in some cases, to improve the appearance of fire scarred slopes (USDA 1995). The evidence that such seeding appreciably reduces significant erosion, however, remains controversial (Krammes and Hill 1963; Taskey et al. 1989; USDA 1990*b*).

Given that seeding after fire is widespread, it is worth asking how this practice influences the re-establishment of native plant species. Two questions were addressed in this investigation.

(1) How well do native plants recolonize sites burned by intense fire?

(2) What are the effects of post-fire seeding of non-native grasses on native plant establishment and recovery?

Although total biotic cover decreases after fires (Agee 1993; Turner et al. 1997), many species resprout vigorously even after intense fires (Lyon and Stickney 1976; Stickney 1986; Turner et al. 1997). Thus, we remain uncertain how changes in fire regimes may affect plants' abilities to recolonize burned sites, and under what conditions seeding would be justified.

Some studies suggest that seeding can affect patterns of native plant recovery (Tiedemann and Klock 1973; Crane et al. 1983; Lyon 1984; Conard et al. 1991). Unfortunately, almost none offer statistical evidence, because of the difficulty of designing experiments around unplanned events (Eberhardt and Thomas 1991), the ubiquity of seeding on burned sites, and the confounding influence of post-fire logging activity. In addition, because seeding after wildfires is treated as an emergency recovery operation, experiments are rarely tried and monitoring is spotty (Agee 1993). It is, therefore, quite difficult to find appropriate control plots within burned and seeded areas. Thus, managers often lack useful information on the ecological effects of post-fire seeding.

To investigate patterns of recovery and recolonization, we examined the distribution and abundance of native plant species 2 years after a crown fire with high forest floor consumption in a dry *Abies grandis* (Dougl.) Lindl. – *Calamagrostis rubescens* Buckl. habitat type in 1996 (Lillybridge et al. 1995). To specifically assess the effect of seeding, we considered it particularly important to compare seeded and unseeded sites. However, because post-fire seeding and salvage logging is so pervasive, we found only a single pair of matched neighboring sites in which to compare seeded and unseeded areas. Both these sites experienced the same fire with similar fire intensity and had not been logged within the last 60 years. They also resemble each other in abiotic character and pre-fire forest composition (see below).

Methods

Study sites and seeding prescription

After extensive field and geographic information system (GIS) searches, primarily within the extensive 1988 Dinkelman Fire and the 1994 Entiat Complex Fires on the Wenatchee National Forest, we were able to locate only a single pair of comparable burned areas where one area was seeded while the other was not. This pair was located on an east-facing slope of Icicle Ridge on the Leavenworth District of the Wenatchee National Forest (T25N R17W, SE1/4 of NE1/4, 47°35′N, 120°42′W). These mid-elevation sites (1000–1220 m) experienced crown fires during the Hatchery Fire in late July 1994. Wischnofske and Anderson (1983) document that historical frequent, low-intensity fires were the typical fire regime for similar dry *Abies grandis* sites adjacent to the 1994 Hatchery fires.

Most upland forest sites within the Hatchery fire were aerially seeded by helicopter in September 1994 with an annual grass, *Triticum aestivum* L. (soft white winter wheat), a short-lived perennial, *Agropyron trachycaulum* (Link) Malte (slender wheatgrass), and a nitrogen-fixing legume, *Trifolium repens* L. (red cover) at a rate of 47.2 kg/ha, with *Triticum aestivum* comprising 80% of the mix; the perennial grass, 15%; and the legume, 5%. We demarcated two study areas of about 7 ha each located on the same east-facing burned slope, one of which remained unseeded because of the presence of a sensitive Cooper's hawk nest. We selected these two particular 7-ha areas because they shared similar forest types, physiographic features (including slope, aspect, elevation, and soils), fire intensity, history of management, and an absence of subsequent post-fire salvage logging. The two areas were less than 1 km apart and separated by a mosaic of burned and unburned forest. The sandy loam soil present throughout the study area is deep and well drained, with slow to medium runoff under an intact forest canopy (USDA 1990*a*).

Sampling procedure

To compensate, in part, for the lack of suitable sites for multiple comparisons, we extensively sampled the vegetation within both 7-ha sample areas and performed several statistical tests (see below) to distinguish the effects of seeding from several potentially confounding local site factors (aspect, elevation, slope, percent open sky, percent soil moisture, and pre-fire stand composition). To sample each area, we first constructed a rectangular grid with 150 potential 15 × 15 m plots, each spaced 50 m apart. We then randomly selected 32 of these in each area, subject to the following constraints: (*i*) we avoided plots with rock outcrops and areas of high soil disturbance (e.g., tree tip-ups) where potential vegetative cover was reduced; (*ii*) we avoided plots where green needles remained on the trees or where the trees had died but the trunks remained unburned above 5 m (to reduce small-scale variation in fire intensity), and (*iii*) we chose plots with similar stocking densities of trees and saplings (to minimize differences in pre-fire understory communities). These efforts appeared successful in that there were no significant differences in the average number of trees or saplings between seeded and unseeded plots (Table 2).

Within each 15 × 15 m (225 m^2) plot, we first characterized the forest community by recording species and diameter at breast height (DBH) for each pre-fire tree (standing or fallen) and percent cover for all woody shrubs >1 m tall. To assay the understory, we used eight randomly placed 1-m^2 subplots to subsample each plot. In each, we estimated percent cover for each forb and grass species and all shrubs <1 m tall. We averaged data from the eight subplots to estimate average cover per plot for each species and tallied the total number of species to gauge richness per plot.

To characterize abiotic site conditions, we measured slope and aspect for each plot and estimated light availability using the average of four sets of readings from a spherical densiometer in each plot. To estimate percent soil moisture, we took one soil sample from each plot at a depth of 20 cm below the organic horizon within a 24-h period following five dry-weather days in mid-July. The samples were weighed, dried for 24 h at 125°C, and then re-weighed, allowing us to calculate the percent change in soil mass due to water.

Table 1. Comparison of abiotic site characteristics from seeded and unseeded treatments.

	Unseeded	Seeded	F	p
Elevation (m)	1163 (74)	1219 (86)	7.54	0.008**
Aspect (°)	94 (12)	86 (16)	5.20	0.025*
Slope (°)	34 (4)	33 (4)	2.39	0.127
Percent soil moisture	3.4 (0.1)	3.9 (0.2)	1.39	0.242
Percent open sky	74 (10)	76 (11)	0.60	0.439

Note: Values are means with SD given in parentheses. *, $p < 0.05$.; **, $p < 0.01$.

Data analysis

Our primary interest was to test the hypotheses that there were no significant differences in total plant cover, native plant cover, species frequency, and species richness between the seeded and unseeded areas (considered a fixed effect). Despite our attempts to choose otherwise comparable areas, the two areas sampled could differ systematically in one or more respects other than the seeding treatment. Thus, any comparison between the two sets of plots should attempt to control and compensate for as many of these potentially confounding factors as possible. We attempted to do so by conducting both simple analyses of variance (ANOVAs) and more complex multivariate analyses of covariance (ANCOVAs), which incorporated the effects of the measured abiotic and biotic variables (SPSS, Inc. 1994). In these ANCOVAs, any differences between the two groups of plots attributable to systematic differences in the measured covariates is controlled for before testing for a significant difference between the seeded and unseeded plots. All tests were evaluated at the 95% significance level.

To decide which biotic and abiotic variables to include as covariates in the ANCOVAs, we considered four criteria: (*i*) those variables found to differ significantly between the two areas based on ANOVAs; (*ii*) any variables found to be significant in explaining variation in native species cover across all plots; (*iii*) any variables significantly related to variation in total cover; and (*iv*) those variables significantly related to native species richness in a simultaneous multiple regression. There were no significant correlations between the independent variables used in the ANCOVAs. Statistics from ANCOVAs were compared with the original ANOVAs to determine if any of the apparent differences between seeded and unseeded areas could be attributed to systematic differences in these environmental variables. We also tested for factor (seeding treatment) by covariate interactions, but none of these proved significant.

To analyze whether artificial seeding affects particular species, we tested for significant differences in mean cover and frequency for each species in seeded versus unseeded plots via *t* tests. This allowed us to distinguish whether each species showed significant changes in cover or frequency in response to the seeding treatment. We only report significant differences for species that are common to (species with frequencies >40%) and well represented in (species with the 10 highest average percent cover values) both areas to ensure that we report on the effects of treatment rather than any slight differences in community composition between areas.

We also explored the degree to which such species' differences might reflect functional characteristics of species groups. We did this by categorizing native plant species according to their post-fire colonization strategy, life history, and stature, then testing to see whether seeding exerted a systematic effect on the species in each functional group. We classified 90% of the species (accounting for 99% of the vegetative cover) by their primary and secondary post-fire colonizing strategies (see Hitchcock and Cronquist 1973; Crane et al. 1983; Rowe 1983; Amour et al. 1984; Stickney 1986; Noste and Bushey 1987; Steele and Geier-Hayes 1992, 1995). Within each plot, we summed the cover and frequency values for all species within each functional group to compare seeded and unseeded area means for each group using *t* tests.

We also classified all species as either annuals, perennials, or biennials (see Hitchcock and Cronquist 1973) and recorded the stature of each species as either short (<10 cm), medium (11–50 cm), or tall (>50 cm) based on average leaf height from field observations and voucher specimens collected from the study area. These tests were similar to those for functional groups, in that we summed the cover and frequency for all species per plot under each life-history category or stature class and then tested for differences in these totals between seeded and unseeded areas using *t* tests.

Results

Similarity in site conditions

Our efforts to choose sites with essentially similar environmental conditions and initial vegetative cover appear to have been successful. Plots in the seeded area were on average 56 m higher in elevation (<5%) and had only a slightly (8°) more northeasterly aspect than plots in the unseeded area (Table 1). The two sets of plots did not differ in average slope, soil moisture, or percent open sky (Table 1). They also matched each other in terms of the average numbers of trees and saplings and total basal areas for each of the dominant species (Table 2).

Differences in overall plot cover and diversity

Plots in the seeded burned area did not significantly differ from plots in the unseeded area in terms of total plant cover, either before or after controlling for variability in local site conditions (ANOVA and ANCOVAs, respectively; Table 3). While plots in the unseeded area initially appeared to have slightly more native species (simple ANOVA; Table 3), the significance of this difference disappears once covariates accounting for environmental differences are included (ANCOVA; Table 3). Such a result suggests success in controlling for the effects of potentially confounding variables.

In contrast to analyses of total cover and species richness, analyses of the total native plant species cover indicates that artificial seeding reduced native plant cover almost by half (Table 3). This difference is highly significant both before controlling for local site variables (ANOVA) and after controlling for the two variables that proved significant in a multiple regression (plot slope and average DBH; second ANCOVA). This difference is somewhat reduced in magnitude (to a 36% reduction in cover) and significance when environmental variables significantly different between the two treatments are included as covariates (first ANCOVA). However, none of these covariates are significant in the multivariate ANCOVA (despite being individually significant in univariate comparisons between plots from the two areas). Such reductions in the magnitude and significance of the

Table 2. Comparison of stand structure for the seeded and unseeded treatments.

	Unseeded		Seeded			
	Mean (SD)	Range	Mean (SD)	Range	F	p
Mean number of stems per hectare						
ABGR	678 (327)	133–1422	512 (298)	78–1216	1.37	0.245
PSME	169 (142)	0–489	254 (224)	0–941	4.73	0.034*
PIPO	42 (39)	0–133	72 (56)	0–274	4.06	0.048*
Total	889 (305)	444–1511	838 (367)	235–1529	0.45	0.505
Saplings	5.8 (6.8)	0–27	8.0 (8.7)	0–34	2.25	0.138
Total basal area (m^2) per hectare						
ABGR	19.8 (12.3)	4.8–55.9	17.3 (14.7)	0.9–56.1	1.19	0.278
PSME	20.8 (19.3)	0.0–71.3	19.5 (15.8)	0.0–75.8	0.38	0.538
PIPO	4.7 (8.4)	0.0–26.1	3.8 (5.3)	0.0–19.4	0.04	0.845
Total	45.4 (21.5)	6.4–93.8	40.6 (14.7)	16.0–80.7	1.95	0.167

Note: Saplings are those trees of 1.0 in. (1 in. = 2.54 cm) DBH. ABGR, *Abies grandis*; PSME, *Pseudotsuga menziesii*; PIPO, *Pinus ponderosa*. *, $p < 0.05$.

Table 3. Analyses of variance (ANOVA) and covariance (ANCOVA) of aggregate response variables among seeded and unseeded burned plots: total biotic percent cover, native species richness (diversity), and percent cover of native species.

		Mean (ANOVA) or adjusted mean (ANCOVA)		
Dependent variable and type of analysis		Unseeded treatment	Seeded treatment	p
Total plant cover (%)				
ANOVA		41.5	48.0	0.194
ANCOVA	Covariates[†]	38.0	40.8	0.640
ANCOVA	Covariates	41.1	38.2	0.288
Native species richness				
ANOVA		17.0	14.8	0.019*
ANCOVA	Covariates[†]	16.7	15.1	0.105
ANCOVA	Covariates[†]	16.2	15.6	0.458
Plant cover of native species (%)				
ANOVA		41.5	21.1	<0.001***
ANCOVA	Covariates	38.7	24.6	0.022*
ANCOVA	Covariates[†]	40.1	21.5	<0.001***

Note: Simple ANOVAs are presented, followed first by ANCOVAs that incorporate all environmental variables that differed significantly between the seeded and unseeded plots (as revealed by ANOVAs). These covariates are aspect, elevation, number of *Pseudotsuga menziesii* stems per hectare, number of *Pinus ponderosa* stems per hectare, and average DBH. The second ANCOVAs include only those local environmental variables found to be significant in multiple regressions for that particular dependent variable, namely percent open sky, slope, number of *Pseudotsuga menziesii* stems per hectare, and average DBH; slope, number of *Pinus ponderosa* stems per hectare, and elevation; and slope and average DBH. *, $p < 0.05$; ***, $p < 0.001$.
[†]Significant covariate effect ($p < 0.05$).

difference, therefore, may reflect only the expected statistical effect of using more predictor variables.

Individual species responses

Although total cover and overall species richness were not affected by seeding, many individual species apparently respond to artificial seeding following fire (Tables 4 and 5). As expected, the seeded species had high frequency and cover on the seeded sites. The annual seeded grass, *Triticum aestivum*, occurred in 94% of the plots in the seeded area, while the perennial grass *Agropyron trachycaulum* occurred in 88%. The seeded legume, *Trifolium repens*, however, occurred in only 9% of the seeded plots. None of these three seeded species appeared in any of the plots in the unseeded areas.

In contrast, most native species either did not change much or significantly decreased in abundance in response to seeding. Of the 60 species sampled in this study, 40 species (67%) occurred in both treatments. Among the 13 most abundant native species (measured by average frequency greater than 40%), five occurred more frequently in the unseeded plots, and six species were equally distributed in both. Only one native species (*Gayophytum diffusum* T. & G.) occurred significantly more frequently in the seeded area (Table 4). Tree seedlings occurred almost twice as often in the unseeded area ($p = 0.012$). Although shrubs less than

Table 4. Frequencies for individual species in seeded and unseeded areas.

	Unseeded treatment	Seeded treatment	p
Native species			
Ceanothus velutinus Dougl.	1.00	1.00	—
Carex geyeri Boot	0.96	0.90	0.309
Lactuca serriola L.	0.90	0.87	0.694
Salix scouleriana Barratt	0.96	0.78	0.023*
Apocynum androsaemifolium L.	0.96	0.75	0.004**
Epilobium angustifolium L.	0.96	0.75	0.011*
Arenaria macrophylla L.	0.87	0.72	0.124
Calamagrostis rubescens Buckl.	0.65	0.84	0.086
Epilobium minutum Lindl.	0.78	0.47	0.009**
Tree seedling	0.68	0.37	0.012*
Cryptantha torreyana Gray (Greene)	0.53	0.37	0.216
Gayophytum diffusum T. & G.	0.28	0.56	0.023*
Collomia tenella Gray	0.31	0.50	0.131
Seeded species			
Triticum aestivum L.	0.00	0.93	<0.001***
Agropyron trachycaulum (Link) Malte	0.00	0.84	<0.001***

Note: All species with frequencies >40% are shown, based on the 32 plots per treatment. The p values are significance levels of individual t tests. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Table 5. Average percent cover for individual species in seeded and unseeded areas.

	Unseeded treatment	Seeded treatment	p
Native species			
Epilobium angustifolium	13.8	2.5	<0.001***
Phacelia hastata Dougl. ex Lehm.	7.4	4.7	0.162
Calamagrostis rubescens	1.8	5.4	0.002**
Apocynum androsaemifolium	4.3	0.4	<0.001***
Ceanothus velutinus	3.4	0.3	<0.001***
Carex geyeri	1.8	1.7	0.837
Lupinus spp.	0.4	3.1	0.021*
Lactuca serriola	2.9	0.3	0.001**
Arenaria macrophylla	1.6	0.5	0.005**
Salix scouleriana	1.5	0.5	0.008**
Pachistima myrsinites (Pursh) Raf.	1.0	0.5	0.209
Arnica cordifolia L.	0.3	0.5	0.488
Collomia tenella	0.2	0.6	0.136
Seeded species			
Triticum aestivum	0.0	11.9	<0.001***
Agropyron trachycaulum	0.0	4.2	<0.001***

Note: Species with the 10 highest mean percent cover values within each treatment are shown based on the 32 plots per treatment. The p values are significance levels of individual t tests. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

1 m tall have 81% less cover in the seeded plots, shrubs greater than 1 m tall show no apparent response to seeding. These results suggest that species that recolonize after fire are affected more by artificial seeding than species that persist at a site after fire (see below). Four additional species differed in frequency between areas, but these species had very low frequency (less than 15% of the plots). Because these species showed no consistent trends of being more frequent in either area, it is difficult to draw any conclusions.

Several fairly predominant native plants also showed pronounced reductions in percent cover in plots from the seeded area (Table 5). Here we compared the 10 native species with the highest average cover from each area, resulting in a total of 13 species. *Ceanothus velutinus* Dougl., the most abundant species occurring in all plots from both areas, showed a 92% decline in seeded relative to the unseeded plots. Six native species had significantly lower cover in the seeded plots, two native species had higher cover in the seeded plots, and five species showed no difference. *Epilobium angustifolium* L., *Apocynum androsaemifolium* L., and *Salix scouleriana* Barratt had both significantly lower frequency and cover in the seeded plots.

Table 6. Comparison of average percent cover for species grouped by their recolonization strategy in seeded and unseeded areas, based on 32 plots per treatment.

	Unseeded treatment	Seeded treatment	p
Resprouters	4.3	3.7	0.364
Off-site colonizers	5.3	1.4	<0.001***
On-site colonizers	0.92	0.13	<0.001***

Note: The p values are significance levels of individual t tests. ***, $p < 0.001$.

Functional group responses

Individual species' responses to artificial seeding often appear to reflect their post-fire recolonization strategies (sensu Rowe 1983). Forty-four percent of the native species found in this study persist at a site by resprouting (resprouters) while 10% germinate from seeds buried in the soil after being scarified by fire (on-site colonizers). About 36% of the native species colonize after burns from off-site seed sources (off-site colonizers). Artificial seeding significantly reduced the cover of on-site and off-site colonizers, whereas the cover of resprouters remained relatively unchanged (Table 6). This suggests that resprouting species compete better with seeded grasses than newly established seedlings do. The frequency of off-site colonizers also decreased in apparent response to seeding (t test, $p = 0.002$), while the frequency of on-site colonizers and resprouting species remained relatively unchanged. Based on combined decreases in cover and frequency, species that disperse onto sites via windborne seeds decrease disproportionately with seeding, perhaps reflecting competitive effects. These off-site colonizing species represent 41% of the native cover in the unseeded sites.

Strategies of recolonization following fire appear to be more useful than either life history or stature in predicting how a species will respond to artificial seeding. Of the 60 species encountered, 77% were perennials, 20% were annuals, and 3% were biennials. Surprisingly, seeded plots did not show any regular decrease in cover or frequency by annuals or biennials. Perennials also showed no collective response to seeding. Similarly, short-statured species were not significantly less abundant in the seeded plots.

Discussion

Native plants can successfully recolonize sites after high-intensity burns in *Abies grandis* forest types that historically experienced mostly low-intensity fires. These plants resprout from roots and underground stems following the fire, recolonize via wind-dispersed seeds, or germinate from seeds scarified by fire. The lack of any statistically significant difference in total plant cover between seeded and unseeded plots suggests that seeding after fire in this forest type may do little to reduce soil erosion, although erosion was not measured in this study. The total cover provided by native plants in our unseeded study plots meets the rehabilitation objectives defined by the Forest Service (USDA 1978) and indicates that even high-intensity fire does not preclude successful local regeneration of the native vegetation.

The artificial seeding of non-native grasses into this *Abies grandis* forest recovering from a high-intensity fire dramatically affected both native plant cover and patterns of relative abundance. Seeding reduced native plant cover by half two seasons after fire despite the fact that total cover was unaffected. This suggests that the seeded grasses directly usurp resources that might otherwise be used by native plants. The slight apparent decline in native species richness in the seeded plots was not significant once site variables were included via the ANCOVAs.

Studies in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.; Conard et al. 1991), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; Crane et al. 1983; Geier-Hayes 1995) and chaparral habitats (Corbett and Green 1965; Nadkarni and Odion 1986) show similar strong decreases in native plant cover with artificial seeding. In a comparable *Abies grandis* forest, Leege and Godbolt (1985) found no significant difference in total cover between seeded and unseeded plots during any of the 3 years after fire. Other studies have further shown that seeding may not effectively mitigate the highest pulse of erosion, which tends to occur just after a fire and before seeded grasses have time to establish (Krammes 1960; Boyle 1982; Wright et al. 1982; Wells 1986) or during intense storms (Krammes and Hill 1963; USDA 1990*b*). Roby (1989) found no significant difference in erosion between seeded and unseeded areas in a Sierra Nevada coniferous forest, yet both areas experienced increased erosion from pre-fire levels. Thus, seeding has questionable efficacy as a significant erosion mitigation technique.

Seeding most dramatically reduced the cover and frequency of early successional species that rely on wind-dispersed seeds to establish. This could reflect either the ability of seeded grasses to pre-empt open sites that might otherwise have been available for colonization or the tendency of these grasses to shade and suppress young colonists. Seeding also reduced the cover of fire-dependent on-site colonizers by more than half. Fire events apparently provide infrequent opportunities for early successional off-site colonizers and on-site colonizers to maintain viable populations across the landscape. Dense post-fire seeding appears to effectively displace several of these species. Because these early successional species occupy an ephemeral position in the post-fire community, they may not benefit from the subsequent decreases in dominance expected in the seeded grasses.

Seeding also reduced the cover and frequency of many late-successional species that resprout after fire. Steele and Geier-Hayes (1992, 1995) classify many of the species in this study (*Apocynum androsaemifolium*, *Arenaria macrophylla* Hook., *Arnica cordifolia* Hook., *Calamagrostis rubescens*, *Carex geyeri* Boot, *Lupinus* spp., *Penstemon* spp., *Pteridium aquilinum* (L.) Kuhn, *Salix scouleriana*, *Spiraea betulifolia* Pall., and *Vaccinium* spp.) as important understory components of mid- and late-successional *Abies grandis* and *Pseudotsuga menziesii* forests. Aside from *Calamagrostis rubescens*, a dominant grass that seeds prolifically with abundant sunlight, this group of mid- to late-successional species experienced a 50% decrease in cover in the seeded area relative to the unseeded area. Thus, by reducing late-successional species, seeding could significantly

alter successional dynamics, resulting in long-term impacts on community character and development.

Lactuca serriola, a naturalized European plant common to areas disturbed by fire and or soil scarification (Hitchcock and Cronquist 1973), also exhibited reductions in cover in response to seeding. Although intense fire can promote the establishment of exotic off-site colonizers in managed forests (Arno et al., in press), seeding in this study appeared to mitigate the invasion of this wind-dispersed exotic. Further long-term research in this area is needed to weigh the relative effects of seeding on both native and non-native establishment.

Site factors and potential pseudoreplication

Are these several biologically and statistically significant differences truly attributable to the artificial seeding or is it possible that the seeded and unseeded areas differed in some systematic way that affected our results? Hurlbert (1984) reviewed the problem that pseudoreplication presents in many ecological studies and cautioned against clustering sample plots in such a way that their responses are not independent (that is, making it difficult to distinguish the effect of a "treatment" from some other systematically varying geographic factor). In this study, the uncontrolled distribution of fire and artificial seeding across the landscape presented us with little choice about where to distribute our study plots. In analyzing the effects of natural disturbance, therefore, the only true level of independent replication is the disturbance event (Wiens and Parker 1995). However, effective strategies can be employed to address the potential problem of pseudoreplication and to provide much-needed empirical data (Eberhardt and Thomas 1991). We first chose plots separated by 50 m or more, which ensured that their composition was independent with respect to the finer scale patterning typical of understory vegetation (Palmer 1995). The considerable variation in composition and cover within both the seeded and unseeded areas and the lack of conspicuous associations in composition between nearby plots suggests that this spacing succeeded in generating independent samples. Such separation also ensured relative independence among the plots in terms of their post-fire colonization dynamics (because of both on-site resprouting and off-site colonization). We further chose to concentrate our analysis on composite variables (like total cover by native species) and particular widespread and abundant species that occurred prominantly in both the seeded and unseeded areas, making it unlikely that these variables were geographically clumped or associated primarily with one of the treatments.

We also sought to avoid potential problems of pseudoreplication by measuring many local site variables and incorporating these into multivariate statistical analyses. Analyses of covariance are recommended in assessing the impacts of unplanned events (Wiens and Parker 1995; Gilfillan et al. 1996), as they are specifically designed to control for variation in site variables before testing the effects of the treatment. While we found that some covariate effects are significant, including these covariates did not diminish the significant results for total or native cover between treatments when compared with ANOVA tests on unadjusted means (Table 3). Thus, possible geographically correlated site factors appear to have minimal effects on how plant cover responds to seeding. Collectively, these results make us confident that our results are robust and not an artifact of pseudoreplication.

Conclusions

Land managers have little evidence to date that seeding with non-native grasses serves to appreciably reduce rates of erosion after high-intensity fires. In fact, spontaneous recolonization appeared to provide adequate cover as quickly as artificial seeding in this study. Seeding might still be acceptable as a management technique if it had little impact on native regeneration and served useful aesthetic purposes. This study, however, demonstrates that artificial seeding with exotic grasses tends to disrupt natural patterns of recolonization by native species. Although we only assessed the impacts of seeding at one point, 2 years after fire, our results suggest that seeding may incur a substantial cost in the form of redirecting natural patterns of plant community recovery after fire in this forest type. At this point, it remains unclear whether such effects will diminish over time or cause longer term effects on native plant communities. We, therefore, advocate further research to ascertain longer term effects, ideally with appropriate experimental controls. At the same time, however, we question the continued widespread and routine use of artificial seeding with exotic grasses.

Acknowledgements

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