
Response of Native and Exotic Grasses to Increased Soil Nitrogen and Recovery in a Postfire Environment

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Abstract

Native plant recovery following wildfires is of great concern to managers because of the potential for increased water run-off and soil erosion associated with severely burned areas. Although postfire seeding with exotic grasses or cultivars of native grasses (seeded grasses) may mitigate the potential for increased run-off and erosion, such treatments may also be detrimental to long-term recovery of other native plant species. The degree to which seeded grasses dominate a site and reduce native plant diversity may be a function of the availability of resources such as nitrogen and light and differing abilities of native and seeded grasses to utilize available resources. We tested the hypothesis that seeded grasses have higher growth rates than native grasses when nitrogen and light availability is high in a greenhouse experiment. To determine how differing resource utilization strategies

may affect distribution of native and seeded grasses across a burned landscape, we conducted botanical surveys after a wildfire in northern New Mexico, U.S.A., one and four years after the fire. In the greenhouse study we found seeded grasses to produce significantly more biomass than native grasses when nitrogen and light availability was high. Seeded grasses increased in cover from 1–4 years after the fire only in areas where total soil nitrogen was higher. Increased cover of seeded grasses did not affect recovery of native grasses, but it did lead to reduced native species richness at small scales. The potential negative long-term consequences of seeding with exotic grasses should be considered in postfire rehabilitation treatments.

Key words: light, mixed conifer, pinyon-juniper, ponderosa pine, rehabilitation, richness.

Introduction

In forest and savanna systems of the southwestern United States, perennial grasses often make up a majority of the understory biomass and perform important ecological functions including serving as forage for wildlife, nutrient retention, and soil stabilization (Cooper 1960; McPherson 1997). In these fire-adapted systems, grass production often increases after low-intensity fire because of increased availability of resources such as light and nitrogen (White et al. 1991). However, unnaturally large and severe wildfires, which have become a more common occurrence in the southwest in recent decades (Swetnam 1990), can delay recovery of native grasses because of high fire-induced mortality of individual grasses and seeds (Armour et al. 1984; Vose & White 1987). Delay in native grass recovery leads to an increased incidence of exposed bare soil, which may create opportunities for exotic species to establish (Keeley et al. 2003; Keeley 2004) and can increase the potential for harmful run-off and soil erosion (DeBano et al. 1988).

To mitigate the ecological risks associated with exposed bare soil following intense wildfire and to encourage ecosystem recovery, areas that experience high fire severity are often aerially seeded with grass seed in hopes of rapidly establishing vegetation. In such efforts, exotic grasses and/or cultivars of native grasses (seeded grasses) are often used because they are often available in large quantities, are relatively inexpensive, and at times have growth characteristics that allow them to germinate and establish quickly relative to native species that would recover naturally from the site (Richards et al. 1998; Robichaud et al. 2000). Despite their widespread use, these treatments remain controversial because of their potential to reduce establishment and growth of tree seedlings (Elliot & White 1987; Barclay et al. 2004; Keeley 2004; Kruse et al. 2004), reduce native species richness (Bock et al. 1986; Keeley 2004), and introduce other exotic species through contamination of seed mixes (Barclay et al. 2004; Kruse et al. 2004). It is also unclear whether such treatments are actually effective in reducing the amount of exposed bare soil after wildfires (Robichaud et al. 2000) because agencies do not have effective protocols in place for monitoring treatment effectiveness (United States General Accounting Office 2003). This has led some to question the use of postfire seeding treatments in some cases (Beyers 2004).

Cultivars of native and exotic species are often bred for a variety of characteristics depending on their intended use.

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Grasses with characteristics such as rapid rates of germination and growth and high seed production may be desirable for use in postfire rehabilitation treatments where rapid vegetation recovery is needed to prevent soil erosion. However, these same characteristics may allow them to outcompete native species and prevent natural recovery of these species. Although agency guidelines require that seeding treatments have no negative impact on natural ecosystem structure and function (Interagency burned area stabilization and rehabilitation handbook 2002), the long-term impacts of these species on native species recovery is not well understood. In some cases, seeded grasses have been shown to persist for only a short period of time, having no long-term negative consequences for native species (Barclay et al. 2004). In other cases, highly competitive seeded grasses have persisted and prevented reestablishment of native species (Bock et al. 1986). The degree to which seeded grasses persist and spread in different environments has not been well studied.

Whether or not seeded grasses competitively exclude native grasses may be a function of resource availability and their response to available resources. Native and exotic grasses have been shown to respond differently to available resources such as water, nitrogen, and light due to their differing evolutionary histories (Melgoza et al. 1990; Naumburg & DeWald 1999; Abbot & Roundy 2003; Brooks 2003). Differing resource utilization strategies can ultimately allow one species to competitively exclude another (Brooks 2000; Corbin & D'Antonio 2004; Humphrey & Schupp 2004). We might expect native and seeded grasses to respond differently to available resources, given that cultivars are chosen for their rapid growth rate and high biomass production, traits that suggest an ability to rapidly take up water and nutrients (Grime 1977), whereas native grasses in arid regions are often adapted to conditions of low nutrient availability and thus take up nutrients at slower rates (Grime 1977; Chapin et al. 1986). Based on ecological theory (Chapin et al. 1986) and some evidence (McGraw & Chapin 1989; Rice & Nagy 2000; Brooks 2003; DeFalco et al. 2003), we may expect seeded grasses to be better able to outcompete native grasses in areas with higher availability of resources such as light and nitrogen.

In this study, we examined how seeded and native grasses respond to increasing availability of soil nitrogen and light and how this may affect their competitive ability in different postfire environments. We hypothesized that seeded grasses would have higher growth rates than native grasses when nitrogen and light availability increases because the seeded grasses used in the postfire rehabilitation treatment were cultivars of native and exotic grasses (Table 1). These species were used for their characteristic rapid growth rates and high biomass production, which indicates high rates of nutrient uptake (Grime 1977). We also examined if differing resource utilization capabilities observed in small-scale experiments could explain how seeded and native grasses were distributed across a larger

Table 1. Plant groups used in analysis of data from greenhouse experiment on effects of light and nitrogen on grass dry weight.

Grass Group	Species
Native perennial grasses	<i>Koeleria macrantha</i> and <i>Schizachyrium scoparium</i>
Exotic annual grasses	<i>Hordeum vulgare</i> , and <i>Lolium perenne</i> ssp. <i>multiflorum</i>
Seeded perennial grasses	<i>Bromus carinatus</i> and <i>Elymus trachycaulus</i>

burned landscape. Nitrogen availability is often higher in higher elevation forests in our study area (Gosz & White 1986) and areas that burn under low or moderate fire intensity (Raison 1979). Thus, we expected cover of seeded grasses to be higher than cover of native grasses in such areas. Finally, we examined if seeded grasses persisted and spread up to four years postfire in different environments and how this may affect recovery of native grasses and native plant species richness. Where cover of seeded grasses remained high, we expected there to be lower cover of native grasses and lower native species richness.

Methods

Study Site

This study was conducted at the Cerro Grande burn, which occurred in May 2000 near Los Alamos, New Mexico, U.S.A. (lat 35°52'N, long 106°19'W). The fire burned 17,352 ha in ponderosa pine, mixed conifer, and pinyon-juniper forest types. Mixed conifer forests typically have higher nitrogen availability compared with ponderosa pine or pinyon-juniper forests (Gosz & White 1986). Pinyon-juniper study sites ranged from 2,109 to 2,228 m in elevation. The dominant overstory species in this cover type are Pinyon pine (*Pinus edulis* Engelm.) and One-seed juniper (*Juniperus monosperma* (Engelm) Sarg). The dominant understory species are Blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag ex. Griffiths), Muttongrass (*Poa fendleriana* (Steud.) Vasey), Mountain muhly (*Muhlenbergia montana* (Nutt.) A.S. Hitchc.), and Little bluestem (*Schizachyrium scoparium* (Michx.) Nash). Ponderosa pine study sites ranged from 2,106 to 2,477 m in elevation. The dominant overstory species in this cover type is Ponderosa pine (*Pinus ponderosa* P. & C. Lawson). The dominant understory species are Little bluestem, Blue grama, Mountain muhly, and Prairie junegrass (*Koeleria macrantha* (Ledeb.) J.A. Schultes). Mixed conifer study sites ranged from 2,484 to 2,863 m in elevation. The dominant overstory species in this cover type are Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco), Quaking aspen (*Populus tremuloides* Michx.), White fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), and Ponderosa pine. The understory is mostly composed of shrubs

(*Robinia neomexicana* Gray, *Paxistima myrsinites* (Pursh) Raf., *Quercus gambelii* Nutt. and *Prunus virginiana* L.) and forbs and grass-like plants (*Carex* spp., *Fragaria virginiana* Duchesne, and *Thalictrum fendleri* Engelm. ex Gray). Average annual precipitation in this region ranges from 30 cm in lower elevations to 90 cm at higher elevations (Allen 1989). Most precipitation falls as rain between June and September. The growing season is approximately from May to mid-October. Soil series include anesa, bayo, cabra, comada, emod, kwage, pines, relado, shell, tentrock, and turkey (Nyhan et al. 1978). Although ecological site descriptions prepared by the National Resource Conservation Service do not exist for these soil series, ecological site descriptions for areas with similar soil characteristics, climate, and topography in New Mexico include mountain breaks, mountain loam, mountain malpais, mountain shale, mountain valley, and pine grassland.

Approximately one month after the fire, all areas classified as high or moderate fire severity were aerially seeded with a mixture of four grass species: *Elymus trachycaulus* (Link) Gould ex Shinnars, *Bromus carinatus* Hook. & Arn., *Hordeum vulgare* L., and *Lolium perenne* ssp. *multiflorum* (Lam.) Husnot. Two of the four grasses used in the reseeding efforts were annual grasses exotic to New Mexico (*L. perenne* and *H. vulgare*). The other two seeded grasses were perennial and considered native to New Mexico (*E. trachycaulus* and *B. carinatus*). However, in a related study where we examined unburned areas just outside the Cerro Grande burn of similar soil types, aspect, and slope (M. E. Hunter, Colorado State University, 2001, personal observation) and in an extensive vegetation assessment of burned and unburned areas adjacent to the Cerro Grande burn (Foxy 1994), these species were not encountered. In addition, the seeded grasses are not listed as dominant understory species in appropriate ecological site descriptions prepared by the New Mexico National Resources Conservation Service. Thus, we assumed that all individuals of these species used in the seed mix encountered in the burned area were seeded grasses that came from postfire rehabilitation efforts.

Greenhouse Study

Seeds from six grass species were collected from the Cerro Grande burn area in August 2001, one year postfire. Four of the species had been seeded for purposes of erosion control after the fire (*E. trachycaulus*, *B. carinatus*, *H. vulgare*, and *L. perenne*). Two of these were common native perennial grasses (*S. scoparium* and *K. macrantha*). All grasses are cool-season (C3) grasses except *S. scoparium*, which is a warm-season (C4) grass. All seeds were sown in flats filled with potting soil and placed in a heated greenhouse in fall 2001. Once seedlings established, they were transplanted individually into 12 × 12-cm pots filled with coarse sand and vermiculite mixed in a one-to-one ratio to a depth of 8–10 cm. Sand was washed with water prior to being put into pots. Pots were watered daily and received

up to four hr of supplementary artificial light per day so that plants could receive 12 hr of light per day. Temperature in the greenhouse ranged from 24 to 27°C.

A factorial experiment was designed to determine how the six grass species respond to increased availability of light and nitrogen under the controlled temperature conditions. Light treatments included full and partial sun. Shade was provided by a black-shade cloth placed 0.8 m above the plots, which shaded 63% of incoming light. Nitrogen treatments included low and high additions of nitrogen and a control (no nitrogen addition). Nutrient solutions were made by mixing constant levels of micro- and macronutrients and differing levels of nitrogen in the form of ammonium nitrate (NH₄NO₃). Plants were watered with nutrient solutions once a week for 16 weeks. Each plant in the low-nitrogen treatment received 0.15 g of nitrogen over the course of the study. Each plant in the high-nitrogen treatment received 0.4 g of nitrogen over the course of the study. Plants in the control group received other macro- and micronutrients only (no nitrogen addition). The values for total nitrogen received were based on the range of annual nitrogen mineralization rates found along an elevational gradient in the study area (Gosz & White 1986). At the end of the experiment, above- and belowground plant parts were harvested and placed in a drying oven (75°C) for three days. Total plant dry weight was then recorded for each plant.

Three grass groups were used for analysis based on nativity (native vs. seeded) and duration (annual vs. perennial): seeded perennial grasses, native perennial grasses, and seeded annual grasses (Table 1). Analysis of variance (ANOVA) was used to test for the effect of light (high and low), nitrogen (high, low, and none), and plant group on plant dry weight. All analyses were done using the general linear model procedure (proc glm) in the SAS statistical program (SAS 1999). When effects were significant, means within factors were compared using Fisher's protected least significant difference.

Vegetation Assessment

In the summer 2001, botanical assessments of the burned area in the Cerro Grande fire in Los Alamos, New Mexico, were conducted. Plot locations were chosen in a stratified random manner by forest type (ponderosa pine, mixed conifer, and pinyon-juniper) and fire severity class (high and low) using Arcview GIS software (ESRI 1999) and existing spatial data layers. There were four plots per strata except for the low-severity pinyon-juniper strata, which had two extra plots. In total, we sampled 26 plots. At each random location we established a modified Whitaker plot (Stohlgren et al. 1998). Percent foliar cover of all species was visually assessed to the nearest 1% in ten 1-m² subplots arranged within a 1,000-m² plot. Percent cover of all species was averaged in the 10 1-m² subplots to obtain estimates of foliar cover at the 1,000-m² scale. Cover of all abiotic features (soil, rock, litter, etc.) was

also estimated in the 1-m² subplots. The entire 1000-m² plot was searched for at least 45 minutes to estimate species richness, which was recorded as number of unique species in the 1000-m² plot. In the center of each plot we estimated percent canopy cover from trees and large shrubs by holding a densiometer at chest level and using an average of readings from four cardinal directions. Soil samples were taken from each corner and the center of the plot, pooled, and analyzed for total nitrogen and carbon. Vegetation was sampled in the same plots again in the summer 2004.

In this study the experimental unit represented the randomized plot stratified by fire severity and vegetation type. Data on effects of grass type (native vs. seeded) and year (2001 and 2004) were taken on the same experimental unit and thus could not be considered independent. To account for the lack of independence we analyzed data as a split-split plot (Yandall 1997). Percent foliar cover was the dependent variable, and grass type (seeded and native), year (2001 and 2004), vegetation type (mixed conifer, ponderosa pine, and pinyon-juniper), and fire severity (high and low) were independent variables. In this model, year, vegetation type, and fire severity were fixed effects and grass type \times plot replicate nested within vegetation type \times fire severity was a random effect. All interactions between grass type, year, fire severity, and vegetation type were tested. The fixed and random effects model was tested using the mixed model procedure (proc mixed) in the SAS statistical program (SAS 1999).

Percentage of total nitrogen has been shown to vary by forest type (Gosz & White 1986) and fire severity (Raison 1979); thus, we expected the same to be true in our study area. To verify that total nitrogen changes with fire severity and vegetation type, ANOVA was used to test for the effects of vegetation type, fire severity, and their interaction on total soil nitrogen in 2001. The same model was used to test the effects of vegetation type and fire severity on percent canopy cover. To determine how incidence of exposed bare ground changed over time across the burned landscape, a split-plot ANOVA was conducted with cover of bare ground as the dependent variable, and fire severity, vegetation type, and year as independent variables. Year \times plot replicate nested within vegetation type \times fire severity was treated as a random effect.

High cover of seeded grasses may limit establishment of other species and reduce native species richness. To test the effects of cover of seeded grasses on native species richness, analysis of covariance (ANCOVA) models were used with vegetation type and fire severity as categorical predictors and seeded grass cover as a continuous variable. The response variable was number of native species per plot or subplot. Four separate models were tested for data collected at the subplot (1-m²) and the plot (1,000-m²) scale, and in 2 years (2001 and 2004). At the subplot scale, seeded grass cover was square root transformed prior to analysis to correct for non-normal error distribution.

Results

Greenhouse Study

Sample sizes between species groups were not equal because of mortality of certain grasses over the course of the experiment; thus, type III sums of squares was used to assess significance of treatments. The two native species were combined as a functional group even though they have different photosynthetic pathways. This was justified by the fact that overall biomass between these species was not significantly different ($F = 0.05$, $p = 0.817$). In the ANOVA examining the effects of plant group, nitrogen treatment, light treatment, and their interactions on dry weight, the three-way interaction ($F = 10.05$, $p < 0.0001$) was significant. All plant groups showed significantly higher dry weight with increasing availability of light and nitrogen (Fig. 1). Native grass dry weight was consistently lower than dry weight of all other plant groups for all treatments except the no nitrogen addition treatment. Native grass biomass increased with increasing nitrogen levels only in the high-light treatment. All other plant groups showed higher biomass in both nitrogen and light levels. The magnitude of difference between native grasses and grasses in other plant groups was lower in the low-nitrogen treatments.

Vegetation Assessment

Across the burned landscape, total N (%) varied by vegetation type ($F = 7.27$, $p < 0.01$) but not by fire severity or the interaction between vegetation type and fire severity. Total N was significantly higher on plots in mixed conifer stands ($0.27\% \pm 0.07$ SE) compared with plots in

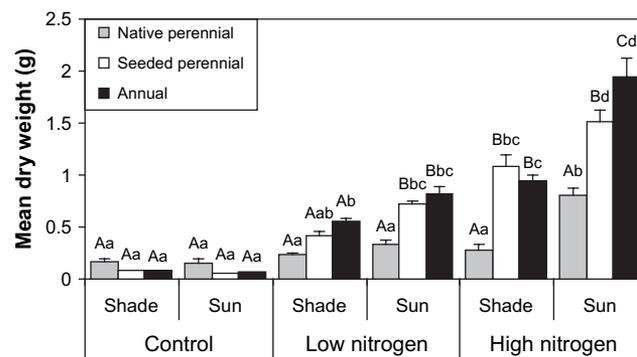


Figure 1. Mean dry weight for grasses from greenhouse experiment in each plant group and each light and nitrogen treatment. Gray bars represent native perennial grasses, white bars represent seeded perennial grasses, and black bars represent seeded annual grasses. Different uppercase letters represent significant differences between means of different plant groups within each treatment group at the $p < 0.05$ level. Different lowercase letters represent significant differences between means of different treatment groups within each plant group at the $p < 0.05$ level. Error bars represent standard error ($n = 303$).

pinyon-juniper ($0.09\% \pm 0.01$ SE) and ponderosa pine ($0.09\% \pm 0.01$ SE) stands.

Canopy cover (%) varied significantly by fire severity ($F = 5.98$, $p < 0.05$), with percent canopy cover significantly lower on high-severity plots ($25.24\% \pm 3.95$ SE) compared to low-severity plots ($41.17\% \pm 6.36$ SE). Percent canopy cover did not vary significantly by vegetation type or by the interaction between fire severity and vegetation type.

In the split-plot ANOVA comparing percentage exposed bare soil versus vegetation type, fire severity class, and year, the interaction between fire severity and year was significant ($F = 5.98$, $p < 0.05$), whereas the interaction between vegetation type and year was not significant. The amount of exposed bare soil was highest in high-severity plots in 2001 (Fig. 2). By 2004, cover of bare ground had decreased in high-severity plots to levels similar to that in low-severity plots.

In 2001, annual and perennial seeded grasses had equal cover across the burned landscape (mean % annual cover = 3.68 ± 0.55 SE; mean % perennial cover = 3.19 ± 0.57 SE). By 2004, seeded perennial grasses persisted and increased in cover across the landscape, whereas seeded annual grasses almost disappeared from the landscape (mean % annual cover = 0.19 ± 0.08). Because we were concerned with how seeded grasses in general would affect native grass recovery across the landscape, we combined annual and perennial seeded grasses in the analysis. It is important to note, however, that most effects would have been from seeded perennial grasses because annual grasses did not persist in the burned landscape. In the split-split plot ANOVA examining the effects of grass type, vegetation type, year, and fire severity on percent foliar cover, the three-way interaction between grass type, fire severity, and year was significant ($F = 3.26$, $p < 0.05$), as was the three-way interaction between grass type, vegetation type, and year ($F = 8.79$, $p < 0.0001$).

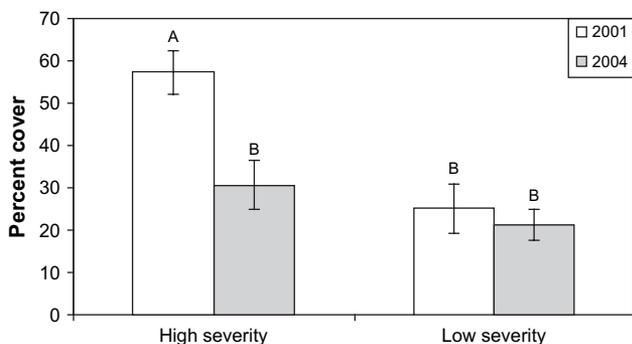


Figure 2. Mean percent cover of exposed bare soil by fire severity class and year. White bars represent percent cover of exposed bare soil in 2001; gray bars represent percent cover of exposed bare soil in 2004. Different letters represent significant differences at the $p < 0.05$ level. Error bars represent standard error ($n = 30$ for low-severity groups, $n = 22$ for high-severity groups).

Cover of seeded grasses did not change from 2001 to 2004 in either fire severity class (Fig. 3). Native grass cover increased from 2001 to 2004 only in areas of low fire severity. Native grass cover was significantly higher than seeded grass cover only in areas of low fire severity in both years. Cover of native grasses was higher in areas of low fire severity compared with areas of high fire severity, whereas cover of seeded grasses was higher in areas of high fire severity compared with areas of low fire severity.

Cover of seeded grasses remained constant from 2001 to 2004 in ponderosa pine stands, decreased in pinyon-juniper stands, and increased in mixed conifer stands (Fig. 4). Cover of native grasses increased from 2001 to 2004 in mixed conifer stands and in ponderosa pine stands but remained constant in pinyon-juniper stands. Cover of native grasses was higher than cover of seeded grasses in 2004 in ponderosa pine and pinyon-juniper stands and in 2001 in pinyon-juniper stands. Cover of seeded grasses appeared higher than cover of native grasses in mixed conifer stands in 2004, but the difference was not significant.

At the 1-m^2 scale, seeded grass cover was square root transformed prior to analysis. This was sufficient for correcting non-normal error distribution, despite the large number of zeros in the dataset. In the ANCOVA model testing the effects of fire severity, vegetation type, and seeded grass cover on native species richness at the 1-m^2 scale in 2001, only vegetation type ($F = 3.04$, $p < 0.05$) and fire severity ($F = 12.40$, $p < 0.001$) were significant effects. Native species richness was significantly higher in areas of low fire severity (4.13 ± 0.24 SE) compared with areas of high fire severity (2.87 ± 0.18 SE) and in mixed conifer (3.85 ± 0.29 SE) and pinyon-juniper forests (4.03 ± 0.26 SE) compared with ponderosa pine forests (2.64 ± 0.25 SE). In 2004 at the 1-m^2 scale, vegetation type ($F = 23.62$,

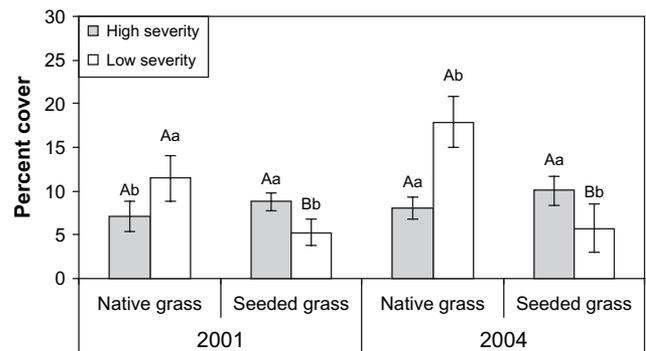


Figure 3. Mean percent cover of native and seeded grasses by fire severity class and year. Gray bars represent percent cover of grasses in high-severity plots; white bars represent percent cover of grasses in low-severity plots. Different uppercase letters represent significant differences for native or seeded grasses between year and fire severity groups at the $p < 0.05$ level. Different lowercase letters represent significant differences between native and seeded grasses within a fire severity and year group at the $p < 0.05$ level. Error bars represent standard error ($n = 12$ for high-severity groups, $n = 14$ for low-severity groups).

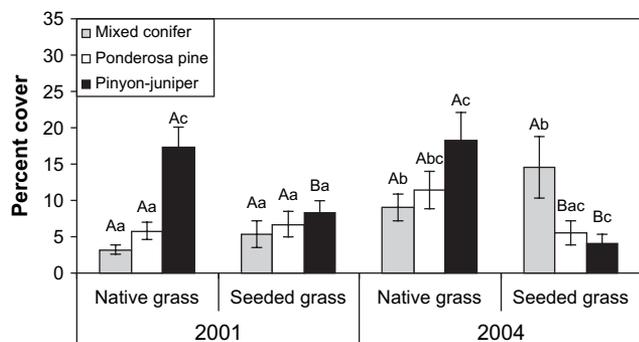


Figure 4. Mean percent cover of native and seeded grasses for different vegetation types in each year. Gray bars represent percent cover of grasses in mixed conifer plots; white bars represent percent cover of grasses in ponderosa pine plots; black bars represent percent cover of grasses in pinyon-juniper plots. Different lowercase letters represent significant differences for native or seeded grasses between year and vegetation type groups at the $p < 0.05$ level. Different uppercase letters represent significant differences between native and seeded grasses within a vegetation type and year group at the $p < 0.05$ level ($n = 8$ for mixed conifer and ponderosa pine groups, $n = 10$ for pinyon-juniper groups). Error bars represent standard error.

$p < 0.001$) and seeded grass cover ($F = 6.51, p < 0.05$) were significant effects. Native species richness was higher in mixed conifer forests (4.85 ± 0.40 SE) compared with ponderosa pine (2.50 ± 0.21 SE) and pinyon-juniper forests (3.33 ± 0.21 SE). Native species richness was negatively correlated with seeded grass cover across all vegetation types. However, this relationship appears to be driven by results in mixed conifer plots (Fig. 5). When separate linear regression analyses were conducted, the negative correlation between native species richness and seeded grass cover was only significant for mixed conifer plots (Fig. 5). In 2001 and 2004 at the 1,000-m² scale, no effects in the models were significant.

Discussion

Seeded annual and perennial grasses produced more biomass with increasing availability of light and nitrogen compared with native grasses, especially in high-nitrogen treatments. This confirms that seeded grasses used at the Cerro Grande fire are able to more rapidly utilize available nutrients than native species in this area. Based on these results, we might expect seeded and exotic grasses to persist and outcompete native species in areas where availability of nitrogen and light is high. This would be consistent with other studies that have shown that exotic grasses are able to produce more biomass and outcompete native grasses adapted to low nutrient conditions in areas with high nitrogen availability (McGraw & Chapin 1989; Rice & Nagy 2000; Brooks 2003; DeFalco et al. 2003). In our study system, this corresponds to mixed conifer stands (high nitrogen) and areas that burned under high fire severity (high light).

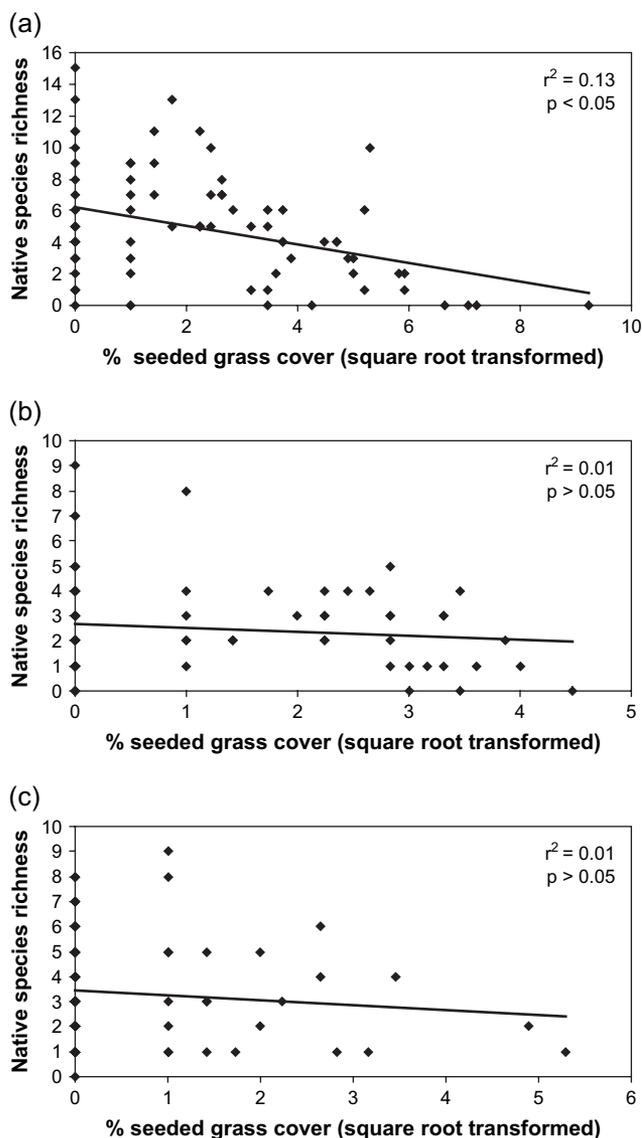


Figure 5. Scatterplot of seeded grass cover (square root transformation) and native species richness at the 1-m² scale in 2004 in (a) mixed conifer plots, (b) ponderosa pine plots, and (c) pinyon-juniper plots.

Interpretations of results from the field study are somewhat difficult because of the lack of an unseeded control area. This is a common problem in studies examining post-fire seeding treatments because managers often do not leave areas unseeded to monitor treatment effectiveness (United States General Accounting Office 2003). However, our results provide important information on where native species recover and seeded grasses persist after wildfires. Although we did not directly study the effects of seeding on native species, the trends we report suggest important relationships and direction for further study.

From 2001 to 2004, cover of seeded grasses increased substantially in mixed conifer stands, corresponding to areas of high total nitrogen. Similar increases in cover were not seen in areas of high fire severity, which corresponded

to high light availability. Seeded grass cover decreased over time only in areas of low total nitrogen (pinyon-juniper stands). Thus, across the burned landscape, nitrogen seems to be a more important factor than light for the persistence of seeded grasses. Other factors that covary with nitrogen availability, such as water availability and temperature, may also be important drivers of seeded grass cover.

If seeded grasses deterred establishment of native grasses, we would expect increased cover of seeded grasses from 2001 to 2004 to coincide with decreased cover of native grasses. Based on this assumption, seeded grasses do not seem to affect native grass recovery. Native grass cover did not change significantly in areas of high fire severity from 2001 to 2004. It did, however, increase in areas of low fire severity. Lack of recovery in high fire severity areas is likely due to the lingering effects of increased fire-induced mortality in these areas and not from competitive exclusion of seeded grasses because cover of seeded grasses did not change over time in areas of high fire severity. Native grasses also increased in cover in mixed conifer stands from 2001 to 2004 despite an increase in seeded grass cover. A similar increase in cover was not seen in pinyon-juniper stands; however, cover of native grasses in pinyon-juniper stands was relatively high one year after the fire. It is unclear, however, how native and seeded grasses will continue to spread in certain areas. Up to four years postfire, plots had up to 30% cover of exposed bare soil, indicating that niches are available for establishment of native and seeded grasses. If seeded grasses continue to spread, this may have negative impacts on native grass recruitment (Hunter 2004).

Increased cover of seeded grasses four years after the fire had some negative consequences for native species richness at small spatial scales. In 1-m² plots, native species richness was negatively correlated with seeded grass cover across vegetation types in 2004. This effect was driven by results in mixed conifer plots, where cover of seeded grasses expanded four years after the fire. Our results show no effect of these factors on species richness at the larger scale, but we feel that we do not have sufficient data to assess species richness at the landscape scale.

Postfire seeding treatments are controversial because of the reported lack of effectiveness in reducing soil erosion (Robichaud et al. 2000), their potential negative impacts on tree seedling recruitment (Elliot & White 1987) and species diversity (Bock et al. 1986), and their potential for introducing other exotic species (Kruse et al. 2004). Although most treatments are applied with the intention that seeded grasses will not persist, lack of persistence of seeded grasses has not been confirmed in many cases (Robichaud et al. 2000; Beyers 2004). In this study, we show that seeded grasses used for postfire erosion control persisted and expanded in areas of high nutrient availability up to four years postfire but did not expand in areas with low nutrient availability. This was consistent with the high biomass production of seeded grasses under high

nutrient conditions observed in the greenhouse study. Although high seeded grass cover does not seem to affect recovery of native grasses, such treatments may result in reduced native plant species richness at least at small scales. Longer-term consequences of seeding treatments are still unknown and warrant study. The potential ecological costs associated with postfire seeding treatments, particularly expansion in areas of high resource availability, should be evaluated in decision-making processes regarding postfire seeding treatments for erosion control.

Implications for Practice

- Seeds from non-native grasses are often applied to severely burned areas to rapidly establish vegetation cover and prevent harmful run-off and soil erosion.
- If non-native grasses persist and spread, they have the potential to prevent native plant recovery and reduce native species richness.
- We found seeded grasses to expand and in cover four years after a wildfire in northern New Mexico in areas where soil fertility was high.
- Higher seeded grass cover corresponded with lower native species richness at small spatial scales, indicating that seeded grasses may have some negative impact on native species recovery after wildfires.
- The potential negative impacts of seeding with non-native species should be evaluated in postfire rehabilitation treatments.

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LITERATURE CITED

- Abbot, L. B., and B. A. Roundy. 2003. Available water influences field germination and recruitment of seeded grasses. *Journal of Range Management* **56**:56–64.
- Allen, C. D. 1989. Changes in the landscape of the Jemez Mountains, New Mexico. Ph.D. dissertation. University of California at Berkeley, Berkeley.
- Armour, C. D., S. C. Bunting, and L. F. Neuenschwander. 1984. Fire intensity effects on the understory in ponderosa pine forests. *Journal of Range Management* **37**:44–49.
- Barclay, A. D., J. L. Betancourt, and C. D. Allen. 2004. Effects of seeding ryegrass (*Lolium multiflorum*) on vegetation recovery following fire in a ponderosa pine (*Pinus ponderosa*) forest. *International Journal of Wildland Fire* **13**:183–194.
- Beyers, J. L. 2004. Postfire seeding for erosion control: effectiveness and impacts on native plant communities. *Conservation Biology* **18**: 947–956.
- Bock, C. E., J. H. Bock, K. Jepson, and J. C. Ortega. 1986. Ecological effects of planting African lovegrasses in Arizona. *National Geographic Research* **2**:456–463.

- Brooks, M. L. 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. *American Midland Naturalist* **144**:92–108.
- Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* **40**:344–353.
- Chapin, F. S., P. M. Vitousek, and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. *American Naturalist* **127**:48–58.
- Cooper, C. F. 1960. Changes in vegetation, structure, and growth of southwestern ponderosa pine forests since white settlement. *Ecological Monographs* **30**:130–164.
- Corbin, J. D., and C. M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for a historical invasion. *Ecology* **8**:1273–1283.
- DeBano, L. F., D. G. Neary, and P. F. Ffolliott. 1988. Fire's effects on ecosystems. John Wiley & Sons, New York.
- DeFalco, L. A., D. R. Bryla, V. Smith-Longozo, and R. S. Nowak. 2003. Are Mojave Desert annual species equal? Resource acquisition and allocation for the invasive grass *Bromus madritensis* subsp. *rubens* (Poaceae) and two native species. *American Journal of Botany* **90**:1045–1053.
- Elliot, K. J., and A. S. White. 1987. Competitive effects of various grasses and forbs on ponderosa pine seedlings. *Forest Science* **33**:356–366.
- ESRI 1999. Arcview GIS software. Environmental Systems Research Institute, Redlands, California.
- Foxx, T. S. 1994. Vegetation succession after the La Mesa fire at Banderlier National Monument. Pages 47–69 in C.D. Allen, editor. Fire effects in southwestern forests: Proceedings 2nd Annual La Mesa fire Symposium. Los Alamos, New Mexico, 29–31 March 1994. USDA Forest Service General Technical Report RM-GTR-286. U.S. Forest Service Rocky Mountain Research Station, Fort Collins, Colorado.
- Gosz, J. R., and C. S. White. 1986. Seasonal and annual variation in nitrogen mineralization and nitrification along an elevational gradient in New Mexico. *Biogeochemistry* **2**:281–297.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**:1169–1194.
- Humphrey, L. D., and E. W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* **58**:405–422.
- Hunter, M. E. 2004. Post-fire grass seeding for rehabilitation and erosion control: implications for native plant recovery and exotic species establishment. Ph.D. dissertation. Colorado State University, Fort Collins.
- Interagency burned area emergency stabilization and rehabilitation handbook, version 2. 2002. URL <http://fire.fws.gov/ifcc/Ers/handbook/> [accessed October 2004].
- Keeley, J. E. 2004. Ecological impacts of wheat seeding after a Sierra Nevada wildfire. *International Journal of Wildland Fire* **13**:73–78.
- Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* **13**:1355–1374.
- Kruse, R., E. Bend, and P. Bierzychudek. 2004. Native plant regeneration and introduction of non-natives following post-fire rehabilitation with straw mulch and barley seeding. *Forest Ecology and Management* **196**:299–310.
- McGraw, J. B., and F. S. Chapin. 1989. Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. *Ecology* **70**:736–749.
- McPherson, G. R. 1997. Ecology and management of North American savannas. University of Arizona Press, Tucson.
- Melgoza, G. R., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire—competition between *Bromus tectorum* (cheat grass) and two native species. *Oecologia* **83**:7–13.
- Naumburg, E., and L. E. DeWald. 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. *Forest Ecology and Management* **124**:205–215.
- Nyhan, J. W., L. W. Hacker, T. E. Calhoun, and D. L. Young. 1978. Soil survey of Los Alamos County, New Mexico. Informal report LA-6779-MS. Los Alamos Scientific Laboratory, New Mexico.
- Raison, R. J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. *Plant and Soil* **51**:73–108.
- Rice, K. J., and E. S. Nagy. 2000. Oak canopy effects on the distribution patterns of two annual grasses: the role of competition and soil nutrients. *American Journal of Botany* **87**:1699–1706.
- Richards, R. T., J. C. Chambers, and C. Ross. 1998. Use of native plants on federal lands: policy and practice. *Journal of Range Management* **51**:625–632.
- Robichaud, P. R., J. L. Beyers, and D. G. Neary. 2000. Evaluating the effectiveness of post-fire rehabilitation treatments. USDA Forest Service General Technical Report RMRS-GTR-63. U.S. Forest Service Rocky Mountain Research Station, Fort Collins, Colorado.
- SAS. 1999. SAS/STAT users' guide. SAS Institute Inc., Cary, North Carolina.
- Stohlgren, T. J., K. A. Bull, and Y. Otsuki. 1998. Comparison of range-land sampling techniques in the Central Grasslands. *Journal of Range Management* **51**:164–172.
- Swetnam, T. W. 1990. Fire history and climate in the Southwestern United States. Pages 7–16 in J.S. Krammes, editor. Proceedings of the Symposium on the Effects of Fire Management of Southwestern United States Natural Resources, 15–17 November 1988, Tucson, Arizona. USDA Forest Service General Technical Report RM-GTR-191. U.S. Forest Service Rocky Mountain Research Station, Fort Collins, Colorado.
- United States General Accounting Office. 2003. Wildland fires: better information needed on effectiveness of emergency stabilization and rehabilitation treatments. Report to Congressional Requesters GAO-03-430. U.S. General Accounting Office, Washington, D.C.
- Vose, J. M., and A. S. White. 1987. Process of understory seedling recruitment one year after prescribed fire in an Arizona ponderosa pine community. *Canadian Journal of Botany* **65**:2280–2290.
- White, A. S., Cook, and J. M. Vose. 1991. Effects of fire and stand structure on grass phenology in a ponderosa pine forest. *American Midland Naturalist* **126**:269–278.
- Yandall, B. S. 1997. Practical data analysis for designed experiments. Chapman & Hall, London, United Kingdom.