DISSERTATION

POST-FIRE GRASS SEEDING FOR REHABILITATION AND EROSION CONTROL: IMPLICATIONS FOR NATIVE PLANT RECOVERY AND EXOTIC SPECIES ESTABLISHMENT

Submitted by:

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WE HERBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISON BY MOLLY E. HUNTER ENTITLED "POST-FIRE GRASS SEEDING FOR REHABILITATION AND EROSION CONTROL: IMPLICATIONS FOR NATIVE PLANT RECOVERY AND ESTABLISHMENT OF EXOTIC SPECIES," BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE DOCTOR OF PHILOSOPHY.

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Abstract of dissertation

Post-fire grass seeding for rehabilitation and erosion control: Implications for native plant recovery and exotic species establishment

Ponderosa pine forests of the southwestern United States are poorly adapted to the high severity wildfires. Such fires result in high mortality of understory species and increase the potential for harmful runoff and soil erosion. To mitigate the risks imposed by high severity wildfire, such areas are often aerially seeded with exotic grasses or cultivars of native grasses in hopes of rapidly establishing vegetation. Despite the wide use of these treatments their ecological effects are not well understood. The purpose of my dissertation is to determine the effects of post-fire grass seeding with exotic grasses and native cultivars (seeded grasses) on native plant recovery and exotic species establishment at the Cerro Grande wildfire in Northern New Mexico. I hypothesize that seeded grasses will dominate over native grasses due to their ability to utilize available resources and their high propagule supply. I also hypothesize that seeded grasses will facilitate establishment of exotic species through contamination of the seed mix with exotic species.

Seeded grasses were found to have much higher seed density than native grasses in the seed bank in areas where they were seeded. This corresponded to higher density of seeded grasses in the above ground vegetation in the same areas. Thus high cover of seeded grasses is likely to be partly due to high propagule pressure. Dominance of seeded grasses over native grasses may also be a function of their higher growth rates in response to availability of nitrogen, as seen in a greenhouse study. This may explain why cover of seeded grasses increased up to four years after the fire in areas where nitrogen availability was high. Seeded grasses did not persist throughout the burned landscape four years after the fire. However, in areas where seeded grasses persisted, lower native grass cover and lower native species richness was found. Even when seeded grasses do not persist on the landscape, they may still pose threats to native plants. Positive correlations were found between seeded grasses and exotic species, perhaps because the seed mixes used in the erosion control treatments were contaminated with seeds of other exotic species. All these results were consistent with my original hypotheses.

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Post-fire grass seeding for rehabilitation and erosion control: Implications for native plant recovery and establishment of exotic species.

Molly E. Hunter

Table of Contents

CHAPTER 1: INTRODUCTION

Wildfire of high severity in southwestern ponderosa pine forests often results in high mortality of overstory and understory species and resultant high cover of exposed bare ground (Armour et al. 1984; Griffis et al. 2001). In addition, high intensity wildfire can result in the development of a hydrophobic layer at or just below the soil surface (DeBano et al.1988). Both fire effects can result in dramatic increases in runoff and soil erosion which pose threats to ecological communities and human life and property. Numerous treatments are implemented immediately after many severe wildfires in hopes of mitigating these threats. One of the most common treatments is application of grass seed (usually aerially) in hopes of rapidly establishing vegetation that will reduce the cover of bare ground and break up the hydrophobic layer (Robichaud et al. 2000). The species used in these treatments are typically exotic or cultivars of native grasses. While these species are usually not considered desirable in the systems in which they are applied, it is assumed that they will not be well adapted to local conditions and thus will not persist, allowing native species to reestablish (Robichaud et al. 2000). It is also assumed that the immediate increase in plant cover will deter establishment of other exotic plants that generally respond positively to disturbance (Beyers 2004). While these treatments are widely used and assumed to be beneficial, the potential exists for these treatments to have negative impacts on ecosystem structure and function including reduced native species richness (Bock et al. 1986; Humphrey and Schupp 2004; Keeley 2004), increased fire frequency (Zedler et al. 1983), encouragement of exotic species establishment (Keeley 2004), and exclusion of native tree and shrub seedlings (Elliot and White 1987; Barclay et al. 2004; Keeley 2004; Kruse et al. 2004). In most systems, these potential negative effects of grass seeding treatments have not been studied.

The few studies that have examined the ecological impacts of seeding with exotic grasses have found both beneficial and detrimental effects of seeding. Seeding with *Lolium multiflorum* (Lam.) was once a common treatment applied to recently burned chaparral shrub stands in southern California (Conard et al. 1995). This grass was found to limit seedling recruitment of annual forbs and shrubs that are adapted to high intensity wildfire (Conard et al. 1995). As a result, these shrubblands were permanently converted to annual grasslands which exhibited lower native species diversity and higher fire frequency than native shrub stands (Zedler et al. 1983). Aside from southern California chaparral, the effects of seeding on native plant recovery are not well understood. In some cases, seeded grasses did not persist in a burned landscape and native species eventually reestablished (Barclay et al. 2004). In other cases seeded grasses dominated and resulted in lower native species richness (Keeley 2004; Kruse et al. 2004). However, long-term studies on the effects of seeding are lacking.

The impacts of grass seeding on establishment of other exotic species (species not used in the seed mix) are not well understood as only a few studies have addressed this question. In most cases exotic plants were less frequently found in areas that were seeded compared to areas that were not seeded after a wildfire (Barclay et al. 2004; Keeley

2004). This was attributed to successful competitive exclusion of exotic species by seeded grasses. Another study found exotic species to be associated with straw mulch used for erosion control (Kruse et al. 2004). This was attributed to contamination of the mulch with other exotic species. Although it has been studied very little, seed mixes also have the potential for contamination with other exotic species.

Overall, the effects of post-fire grass seeding for erosion control on ecosystem properties are poorly understood. Further research is warranted given the wide use of such treatments and their potential for negative impacts on ecosystem structure and function. The purpose of my dissertation research was to examine the impacts of post-fire grass seeding on ecosystem properties, particularly native plant recovery and exotic species establishment. This work was conducted at a large wildfire in northern New Mexico, the 2000 Cerro Grande fire. A majority of the burned area in this fire was heavily seeded with exotic grasses and cultivars of native grasses. I examined the effects of seeded grasses on native and exotic plant species in four integrated studies.

The degree of propagule supply can be an important factor in determining whether an exotic species establishes and dominates (Lonsdale 1999; D'Antonio et al. 2001; Levine 2001). Typically, the more seeds of a species present in a system, the more likely that species will establish and dominate. After wildfires the seed bank of native species is typically depleted and high mortality of individual plants reduces the seed rain (Armour et al. 1984; Vose and White 1987). Low seed input of native species coupled with high input of seeded grass seed could assure that seeded grasses dominate the burned area. In chapter 2, I address the impacts of seed supply on dominance of seeded and native grasses. I examine if seeded grasses dominate the seed bank in areas of different fire severity and if this corresponds to dominance in the vegetation.

High cover of exotic grasses has been shown to inhibit recruitment of native grasses by seed (Brooks, 2000; Humphrey and Schupp 2004), but competitive exclusion may only occur under certain environmental conditions (Corbin and D'Antonio 2004) or may be overcome by high seed input of native species (Seabloom et al. 2003; Mouquet et al. 2004). In chapter 3, I determine how high cover of seeded grasses impacts recruitment of native grasses by seed by manipulating cover of seeded grasses and adding seeds of native grasses in a field experiment.

Exotic grasses that are better adapted to high nutrient conditions often have higher maximum growth rates than native grasses that are adapted to low nutrient environments (Maron and Jefferies 1999; Brooks 2003). This often allows exotic grasses to be superior competitors to native grasses when nutrient availability is high. We might expect grasses used in seed mixes to also be adapted to high nutrient availability given that they receive artificial fertilization throughout their lifetimes. Even native cultivars of grasses often exhibit very different growth rates than local varieties of the same species (Gustafson et al. 2004). Thus, one may expect seeded grasses used for post-fire rehabilitation to exclude native grasses when availability of nitrogen is high. In chapter 4, I determine how native and seeded grasses respond to increasing availability of light and nitrogen in a greenhouse experiment. I then extrapolate the results of the greenhouse study to the burned landscape by determining if availability of light and nitrogen are good predictors for seeded and native grass cover across the burned area. I also determine whether or not seeded grasses persist over time and if this had negative impacts on native species.

Exotic species that are adapted to disturbance are often more likely to establish after a wildfire, especially in areas of high fire severity (Crawford et al. 2001). It is unclear whether seeding with grasses exacerbates spread of exotic species through contamination of seed mixes or prevents their spread through competitive exclusion. In chapter 5, I determine how exotic plant species are distributed across the burned landscape in relation to abiotic factors such as fire severity, elevation, soil nitrogen, and biotic factors such as cover of seeded grasses and native species richness.

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CHAPTER 2: Seed banks of native and cultivated grasses in pine forests of the Cerro Grande fire area of New Mexico.

Abstract

The degree of seed availability in the seed rain or seed bank can be an important indication of potential recovery following a disturbance such as a wildfire. To determine how supply of exotic and cultivated grasses used for post-fire erosion control may disrupt recovery of native perennial grasses following fire, I compared seed banks and vegetation of native grasses and cultivated grasses following the Cerro Grande fire in northern New Mexico, USA. Number of seeds/m^2 of cultivated grasses exceeded that of native grasses in areas of high and moderate fire severity but not in areas of low fire severity ($F = 10.20$, n = 36, df = 2, p = 0.0004). Similarly, there were more cultivated and exotic grass plants/m^2 than native grass plants in areas that burned under high and moderate fire severity ($F = 20.89$, n = 74, df = 2, $p < 0.0001$). To determine how density of seeds from native and cultivated grasses compared to density of above ground vegetation, a similarity index (SI) was calculated. This analysis indicated that SI for cultivated varieties was significantly higher than SI for native grasses in areas of high and moderate

fire severity (*F* = 5.59, n = 36, df = 2, p = 0.009). In areas of low fire severity, native grass SI (0.13 ± 0.08; 1 SE) was statistically equivalent to cultivated grass SI (0.17 ± 0.17; 1 SE). The high SI for cultivated varieties in areas of low fire severity, despite low density in the seed bank, indicates the strong inclination of cultivated grasses to establish as vegetation if they are present in the seed bank. The high number of seeds of cultivated grasses in the seed bank and their strong ability to establish when seeds are present in the seed bank, suggests a potential for cultivated varieties to dominate the burned area at the expense of native grasses.

Introduction

A seed bank can be an important source of recovering vegetation following a disturbance (Parker et al. 1989). Alteration in disturbance regimes can change the density and composition of the seed bank and thus lead to a subsequent change in the above ground vegetation following a disturbance (Archibold 1989). In southwestern ponderosa pine systems (*Pinus ponderosa* P. & C. Lawson), heavy cattle grazing and fire suppression during the nineteenth and twentieth centuries have contributed to increased canopy cover and increased loading of surface fuels (i.e. litter, woody debris); (Covington and Moore 1994). The decreased availability of light and soil resources and decreased availability of suitable microsites for seed germination (due to increased litter loading) have led to a decrease in native grass cover (Cooper 1960; Covington and Moore 1994). Native grass seed banks are typically short-lived and rely on continued seed production from nearby plants (Rice 1989). A reduction in the cover of native grasses should result in reduced seed rain and thus reduced inputs to the seed bank. While there have been no studies that specifically examine the impacts of changing disturbance regimes on seed banks in southwestern ponderosa pine forests, it is reasonable to expect that the density of native grass seed in the seed bank has been reduced along with a decrease in cover of native grasses, given that seed banks of native grasses are typically short lived. Wildfire, particularly of high severity, may further deplete the soil seed bank through increased mortality of seeds in the seed bank and plants which act as seed sources (Korb et al. 2004). Recovery of native grasses in large patches of high fire severity may be further delayed because of long distances from available seed sources.

Lack of understory recovery following wildfire can pose immediate threats to ecological and human communities through increased runoff and soil erosion (DeBano et al. 1988). To mitigate such risks, managers often apply large amounts of grass seed to severely burned areas immediately after wildfire events in hopes of reducing the amount of exposed bare ground. Often non-native grasses or native cultivars (seeded grasses) are used because of their wide availability, low cost, and ability to rapidly establish under a variety of conditions (Robichaud et al. 2000). The same factors that allow these species to establish and grow rapidly, might also allow them to be superior competitors over native species. A competitive advantage for different resources (i.e. water and nitrogen) has been shown to be a factor that results in dominance of exotic grasses at the expense of native grasses (Melgoza et al. 1990; Brooks 2003). Recent studies have shown that increased propagule pressure is another important factor in predicting successful dominance of an exotic plant species (Levine 2001). The possible low density of native grass plants and seed in the seed bank following high severity fires coupled with the application of large amounts of introduced grass seed could cause seeded grasses to dominate the seed bank and the vegetation. If seeded grasses overwhelm the propagule supply (seed rain and seed bank) and are superior competitors over native grasses for available resources, they could dominate post-fire systems for some time. Persistence and dominance of seeded grasses may ultimately prevent native plant recovery, reduce plant diversity, and lead to a site conversion (Griffin 1982; Conard et al. 1995; O'Leary 1995).

Estimating the number of seeds in the seed bank and correlating it to above ground vegetation has proven to be difficult and to vary by factors such as vegetation type and disturbance history (Major and Pyott 1966; Bigwood and Inouye 1988; Benoit et al. 1989). Seed bank density can be highly spatially heterogeneous often with higher density near parent plants (Major and Pyott 1966). Even when estimates of seed density are accurate, the seed bank will not always correspond to what is found in the above ground vegetation (Major and Pyott 1966; Hutchings and Russell 1989). In grasslands, this has been partly attributed to differences in sampling strategies, but also a function of how different species respond to their environment (Rice 1989). For example, cereal grasses often germinate more readily than other grass species under a wide range of environmental conditions and thus may be more likely to have a high correspondence between the seed bank and vegetation (Cavers and Benoit 1989). High correspondence between the seed bank and vegetation can be a good indication of a species' ability to germinate and establish.

In this study, I examined the dynamics of the seed bank and above ground vegetation for seeded grasses and native grasses in a burned ponderosa pine forest in northern New Mexico, USA. I addressed how propagule pressure and competitive ability might vary between native and seeded grasses and how this may impact long-term recovery of native grasses in southwestern ponderosa pine forests after wildfires.

In addition, I used this study as an opportunity to experiment with different methodologies for estimating the number of seeds in the seed bank and their correlation with above ground vegetation. Specifically I addressed the following questions:

How do sampling intensity, scale and spatial patterning of seeds and vegetation influence estimates of seed density in the soil and the correspondence of seed density with the density of above ground vegetation?

Do native or seeded grasses dominate the seed bank and the above ground vegetation in areas of different fire severity and areas that are seeded with exotic or cultivated grasses for erosion control versus areas that are not seeded?

How well does the seed density of native and seeded grasses correlate with density of above ground vegetation in areas of different fire severity?

Study site

This study was conducted at the Cerro Grande burn, which burned 17,352 hectares in May of 2000 near the town of Los Alamos in northern New Mexico, USA (35° 52’ N, 106° 19’ W). The fire burned primarily through ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests. A few weeks after the fire, all areas classified as high and moderate fire severity were aerially seeded with a mixture of four grass species (table

1). Two of these species (*Hordeum vulgare* L. and *Lolium multiflorum* Lam.) are exotic annual grasses while the other two (*Bromus carinatus* Hook. & Arn. and *Elymus trachycaulus* (Link) Gould ex Shinners) are native perennial grasses. The two native grasses used however, while native to the state of New Mexico, are not common grass species in ponderosa pine forests in the southwest and were rare in the study area prior to the wildfire (Foxx 1994). Thus, I assumed that the four species in the seed mix encountered in the study came from the seeding efforts and were not present prior to the wildfire. I made this distinction because cultivated varieties of native grasses are likely to respond differently to available resources than local varieties because cultivated varieties are often bred for rapid germination, high seed production, or disease resistance (Gustafson et al. 2004). I examined these grasses in this study along with four of the most common native perennial grasses in this system (Table 1). Nomenclature follows the Natural Resources Conservation Service Plants database (USDA, NRCS 2004). The seeded grasses in this study do not have persistent seed banks. Thus, I assumed seeds encountered in the seed bank came from grasses that produced seed in previous growing season.

Within the Cerro Grande burned area, I focused my study in Rendija Canyon, which is located adjacent to the town of Los Alamos in the Sante Fe National Forest, New Mexico. Different areas in this canyon experienced low, moderate, and high fire severity all within close proximity to each other. Thus, other variables that may influence the vegetation and seed bank (i.e., distance to roads, elevation, soil type) were relatively constant within the study area. Areas classified as high and moderate fire severity within the study area were aerially seeded for erosion control at a constant rate (about 600 seeds/m^2) within two months of the fire. Areas that experienced low fire severity were not seeded.

Methods

Plot locations were chosen in a stratified random fashion within Rendija Canyon in the Santa Fe National Forest. Three sites were chosen in each fire severity class (high, moderate, and low). Fire severity was assessed using Burned Area Emergency Rehabilitation (BAER) fire severity maps. BAER maps of fire severity are made using post-fire Landsat imagery. I visually verified fire severity levels (high, moderate, and low) by examining tree crown scorch and consumption at each site. High fire severity was classified as areas with complete or near complete consumption of crown needles. Moderate fire severity was classified as areas with partial consumption of crown needles. Low fire severity was classified as areas with scorched needles left on trees. In each plot location (three per fire severity class) one 50-m transect was placed parallel to the line of contour.

To account for potential spatial heterogeneity in the seed bank, I further stratified samples along each 50-m transect. Areas dissected by transects were grouped into patches of bare ground (< 5% vegetative cover) and patches with some grass cover (> 5%). I excluded areas that were dominated by other features (rock, shrubs). A minimum of five grass cover plots and three bare ground plots were randomly sampled along each transect. In the middle of each plot, a soil sample was collected which encompassed a circular area 10 cm in diameter to a depth of 5 cm. I sampled number of individual grasses in the 1-m^2 area around each soil sample. Vegetation measurements were taken in the fall of 2001 (one year post-fire), the spring of 2002 (two years post-fire), and the summer of 2002 (two years post-fire). Plants were marked so that they would not be counted more than once in subsequent samplings. Individual grass plants were easily distinguished as individuals were newly established and thus, rhizomatous spread had been minimal. Soil samples were taken in the fall of 2001 when most of the flowering grasses had dropped their seeds produced in the spring and summer of 2001.

Previous studies have shown disagreement as to the best methodology (i.e., number and spatial patterning of samples) to estimate seed density in the seed bank. Certain authors have suggested that collecting more and smaller samples results in better estimates of seed density (Bigwood and Inouye 1988; Benoit et al. 1989). To better understand how sampling techniques might influence estimates of seed density in this system, I took up to three soil samples per 1-m^2 plot (Figure 1). I then estimated the number of seeds per square meter using one, two and three soil samples. Given my constraints for greenhouse space, I had to limit the number of soil samples taken. Since I assumed that seed density and variability in seed density would be higher in grass cover plots, I collected more samples in grass cover plots (three) compared to bare ground plots (one).

Soil samples collected from plots were placed in a refrigerator (~20°C) for at least two weeks for cold stratification. The soil samples were then laid out in thin layers in flats with potting soil, placed in a heated greenhouse and watered daily. Flats were watered once a week with a Hoagland's nutrient solution. I identified and counted seedlings emerging from flats on a daily basis. This has been shown to be a preferred method for estimating seed density and diversity in seed banks (Gross 1990). I immediately removed identified seedlings from flats. Seedlings that were not easily identified were transplanted into pots and allowed to grow until identifiable. Because a large number of samples are required to assess the seed bank and vegetation of uncommon species (Benoit et al. 1989), I focused measurements on dominant species in this system which included four native and seeded grasses (Table 1).

I estimated the density of seeds/m^2 for different sampling intensities by multiplying the number of seeds in one soil sample (center) by 100, in two soil samples (corners) by 50 and three soil samples by 33.3 (see figure 1). Using two-way analysis of variance (ANOVA) I tested the effect of sampling intensity (one, two or three pooled soil samples) and grass type (seeded and native) and their interaction on density of seeds. I expected the native grass seed bank to be highly spatially variable. Thus, I expected to detect higher density and less variability of seed density when three soil samples were used to estimate seed density per plot. Since seeded grasses were applied at a relatively constant rate, I did not expect the seeded grass seed bank to be highly spatially variable. Thus, I did not expect to see decreasing variability in seeded grass density or increased estimates of density when three soil samples were used to estimate density. The sampling intensity with the highest density of seeds or lowest variability in estimates was then used for the remainder of the analysis.

To examine how spatial patterning may impact estimates of seed density, I used two-way ANOVA to test the effect of grass type (native or seeded), plot type (grass cover and bare ground) and their interaction on estimates of seed density. I expected bare ground plots to have lower density of seeds than grass cover plots. Using two-way ANOVA, I tested the effect of fire severity, grass type and their interaction on estimates of seed density. I expected seeded grasses to have higher density where seeding efforts were focused (high and moderate fire severity areas) and native grasses to have higher density where seed and plant mortality would have been lower (low fire severity areas). I also used two-way ANOVA to test the effects of fire severity, grass type, and their interaction on density of plants in 1-m^2 plots.

Relative seed density and relative plant density was calculated for each species by dividing density of seeds (or plants) from one species by density of seeds (or plants) from all species within a grass group (native or seeded grasses). I calculated relative density for each seed bank sample and vegetation plot at each scale of measurement (one, two, and three pooled soil samples; 60 cm^2 and 1 m^2 vegetation plots). A similarity index (SI) was then calculated based on relative seed and plant density and used to describe the similarity between the seed bank density and above ground plant density (Greig-Smith 1964):

$SI = 2\ w / a + b$ (Eq. 1)

where a is the sum of all values of relative seed density for all seeded (or native) grass species; b is the sum of all values of relative plant density for all seeded (or native) grass species; and w is the sum of the lower relative density values (between the seeds and plants) for all seeded (or native) grass species that are recorded in both the seed bank sample and the vegetation plot. This is similar to methods used by Ungar and Woodell (1996). Species that were not recorded in both the seed bank and the vegetation were not included in w. SI has a range of 0 – 1; SI = 0 indicates no correspondence between the seed bank and above ground vegetation, SI = 1 indicates a perfect correspondence between the seed bank and the above ground vegetation.

To determine if the correspondence of vegetation to seed bank depended on scale of measurement, I measured density of vegetation at two scales, 1-m^2 and 60-cm^2 (figure 1). SI was determined for native and seeded grasses for one soil sample (center) versus the large (1-m^2) plot, one soil sample versus the small plot (60-cm^2), two pooled soil samples (corners) versus the large plot, two pooled samples versus the small plot, the three pooled soil samples versus the small plot, and the three pooled soil samples versus the large plot (see Figure 1). A two-way ANOVA was used to test if SI was dependent on the six different sampling intensities for seed and plant density. Transformation of SI values was not conducted as ANOVA can be robust even when the assumption of non-normal distribution of error values is not met (Quinn and Keough 2002). A two-way ANOVA was conducted to determine if SI depended on the grass type (seeded versus native), fire severity (low, moderate, high), and their interaction. All statistical analyses were conducted using the general linear model procedure (proc glm) in the SAS statistical program for Windows (version 9.1, SAS, 2002-2003, Cary, North Carolina). Treatment comparisons were made using Tukey-corrected p-values with an alpha level of 0.05.

Results

The density of seeds/m^2 varied significantly by grass type (native versus seeded), but did not vary significantly with the number of samples taken per plot nor by the interaction between sample number and grass type (Table 2). Even though the interaction between sample number and grass type was not significant, the variability associated with estimates of native grass density decreased with increasing number of samples taken, while variability associated with estimates of seeded grass density appeared constant (Table 3). Regardless of sampling intensity, density of seeded grass seed was much higher than density of native grass seed (Table 3). Because variability in estimates of native grass seed density decreased when more soil samples were pooled for analysis, I used data from the three pooled soil samples for the remainder of the analysis.

When examining the mean density of seeds per m^2, there was a significant effect of grass type (native versus seeded), fire severity (high, moderate, low), and a significant interaction between grass type and fire severity (Table 4). The mean density of native grass seeds tended to be higher in areas burned under low fire severity, although there is high variation associated with the estimates, and no significant difference in mean density of seeds of native grasses between areas of high, moderate, and low fire severity (Table 5). The trend could suggest that mortality of seeds in the seed bank was lower in areas of low fire severity. The lack of significance was probably due to the high degree of spatial variability in the native grass seed bank. There was significantly higher density of seeded grass seeds compared to native grass seeds in areas of high and moderate fire severity (Table 5). There were very few seeds from seeded grasses in areas of low fire severity probably because application of seed was focused in areas of high and moderate fire severity.

The mean density of plants in large (1-m^2) plots showed similar trends to the seed bank. There was a significant effect of grass type and a significant interaction between grass type and fire severity on the mean density of plants/m^2 but no effect of fire severity alone (Table 6). There were very few native grasses in areas of high and moderate fire severity and significantly more native grasses in areas that burned under low fire severity

(Table 7). I found very few seeded grasses in areas that burned under low fire severity and significantly more seeded grasses in areas that were classified as high or moderate fire severity (Table 7).

Since only one soil sample was taken in plots dominated by bare ground, the center soil sample was used to assess seed density in bare ground versus grass cover plots. In this ANOVA model no effects were significant (Table 8). However, it did appear that density of seeded grass seeds was much higher in grass plots compared to bare ground plots even though differences were not significant (Table 9). In general there was much more error associated with mean number of seeds per sample, possibly because only one soil sample was taken per plot (Table 9).

The index of similarity (SI) between the seed bank and the above ground vegetation did not vary with the six different sampling strategies (F = 1.10, df = 5, n = 168, p = 0.364). However, mean SI tended to increase when more than one soil sample per plot was used and when it was compared to the larger vegetation plot (Table 10). Thus, SI values calculated from use of three pooled soil samples and the large (1-m^2) vegetation plot were used in the remainder of the analysis.

The effect of grass type and the interaction between fire severity and grass type on mean SI was significant but fire severity was not (Table 11). Mean SI appeared to be higher for seeded grasses in areas of high and moderate fire severity compared mean SI for native grasses (Table 12), probably due to the high density of seeded grass plants in areas of high and moderate fire severity (Table 7). There was no significant difference between SI for native and seeded grasses in areas of low fire severity (Table 12). Mean SI for native grass was zero in both high and moderate fire severity plots, even though native grasses were present in both the seed bank and the vegetation (Tables 5 and 7). Mean SI for native grasses was higher in low severity plots, but did not approach levels of SI for seeded grasses in high and moderate fire severity plots (Table 12). There was high variability in mean SI for seeded grasses in low severity plots, probably because of the low occurrence of seeded grass plants and seeds in such areas (Tables 5 and 7).

Discussion

Density of seeds in seed banks can be highly spatially variable due to a variety of factors (Major and Pyott 1966) and my results echo this pattern. Many researchers have attempted to devise sampling strategies that result in more accurate estimates of the density of seeds in the seed bank. Some have suggested that taking more and smaller samples is more effective (Bigwood and Inouye 1988; Benoit et al. 1989). In my study, the estimates for density of seeds/m^2 in the seed bank did not vary significantly with the number of samples pooled per plot. However, the variability in soil seed bank estimates decreased when more soil samples per plot were pooled for analysis, indicating that taking at least three soil samples per plot may be more appropriate in this system for estimating seed density, especially for native grass seeds. Variability in seed bank density did not appear to be a function of distance from parent plants, as there was no significant difference between seed bank density in grass cover versus bare ground plots. However, I found high variability associated with estimates, probably due to the sampling of just one soil sample in bare ground plots. The density of seeded grass seeds appeared to be higher in grass cover plots and I might have detected a significant difference had I collected more soil samples per plot. In grass cover plots, the scale of measurement was not significant when comparing the seed bank to the vegetation, although SI appeared higher with more soil samples and larger vegetation plots, indicating that this sampling scheme may be more appropriate in this system.

The potential exists for native grasses to recover from severe wildfire. Native grass seed was present in the seed bank in all study sites, regardless of fire severity, indicating that seeds were not completely depleted from the burned area due to mortality from the wildfire or that there were remnant seed sources. The presence of viable native seed in the seed bank and remnant plants in the vegetation indicates at least the potential for native grasses to reestablish on site. If recovery was restricted by seed recruitment from off site, recovery would likely be very slow given the large size of the fire and the subsequent distance of available seed sources (van der Valk and Pederson 1989). Density of native grass seed tended to be lower in areas that burned under high and moderate fire severity, indicating that mortality was higher in such areas or remnant living grasses were scarce. The density of native grass plants was low in areas that burned under high or moderate fire severity, regardless of their presence in the seed bank. The density of seeded grass was much higher than that of native grass in areas of high and moderate fire severity, presumably because of the seeding efforts in those areas.

Seeded grasses have a strong tendency for germination and establishment. The high degree of similarity between density of seeded grass seeds and the density of seeded grass plants compared to native grasses indicates that seeded grasses are more likely than native grasses to establish if present in the seed bank. The high correspondence between seeded grass seeds and plants could be due to the high density of seeded grass seeds compared to native grass seeds, or because of characteristics of the species themselves.

Exotic grasses often have less stringent requirements for germination than native grass species in semi-arid regions (Humphrey and Schupp, 2002). We might expect the same to be true for cultivated grasses given that they are often bred to establish rapidly (Gustafson et al. 2004). Other studies have shown that seeded and native grasses in this system have differing responses to resource availability with seeded grasses increasing more in biomass than native grasses when availability of light and nitrogen increases (chapter 4). These traits coupled with the high density of seeds could allow seeded grasses to dominate and persist in such areas and disrupt recovery of native species.

Seed banks and vegetation commonly change with time since disturbance (Pierce and Cowling 1991). Typically seed banks are depleted as a result of fire, but rapidly recover as vegetation reestablishes (Hassan and West 1986; Ferrandis et al. 2001). I expect the same to be true for native grasses in this southwestern ponderosa pine system. However, the high occurrence of seeded grass seed and low occurrence of native grass seed may alter the trajectory of recovery of this system. If seeded grasses dominate the seed bank, are more likely to establish than native grasses, and are more competitive, they may be more likely to dominate the site for several years. This is contrary to the long-term objective of such treatments which is to eventually allow for ecosystem recovery including pre-fire ecosystem functions, structure, and diversity (Interagency burned area stabilization and rehabilitation handbook 2002). The fact that seeded grasses still dominate the seed bank and vegetation up to two years after the treatments suggests that they may persist. In fact, seeded grass cover increased in certain areas up to four years post-fire and this seems to have consequences for native species richness (chapter 4). Persistence and dominance of seeded grasses has been shown to lead to reduced cover of native grasses, reduced plant diversity, reduced survival of tree seedlings, and in extreme cases to complete site conversion (Griffin 1982; Bock et al. 1986; Elliott and White 1987; Conard et al. 1995; O'Leary 1995). Longer term monitoring of seeding treatments should be conducted to assure their effects on ecosystem recovery in different systems are in fact beneficial or benign.

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Figure 1: Sampling design for seed bank and vegetation in the 2000 Cerro Grande burn, NM. Seed bank samples were taken in two corners and in the center of the 60-cm^2 plot. Above ground vegetation was measured in 60-cm^2 plot and the 1-m^2 plot

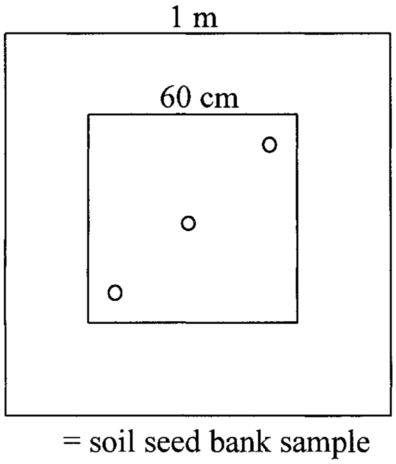

Table 1: Grass species examined in seed bank study within the 2000 Cerro Grande burn, NM. The first four are species used in the aerial seed mix, the last four are the most common native grasses found in the study area.

Species	Classification	Grass type
Hordeum vulgare L.	Seeded	Annual
Lolium multiflorum Lam.	Seeded	Annual
Elymus trachycaulus (Link) Gould ex Shinners	Seeded	Perennial
Bromus carinatus Hook. & Arn.	Seeded	Perennial
Bouteloua gracilis (Willd. Ex Kunth) Lag. ex Griffiths	Native	Perennial
Koeleria macrantha (Ledeb.) J.A. Schultes	Native	Perennial
Muhlenbergia Montana (Nutt.) A.S. Hitchc.	Native	Perennial
Schizachyrium scoparium (Mitchx.) Nash	Native	Perennial

Table 2: ANOVA results of the mean density of seeds per square meter for seeded and native grasses when one, two and three soil samples are collected per plot. N = 108.

Source	F	df	P
Model	4.67	5	0.0007
Sample number	0.35	2	0.7050
Grass type	21.51	1	<0.0001
Sample number X grass type	0.56	1	0.5722

Table 3: Mean estimated seed density and standard error of native and seeded grasses per square meter when one, two, and three soil samples are collected per plot. N = 108. Different letters represent significant differences at the p<.05 level. For native grasses, standard error decreases as number of pooled samples increases.

Number of samples	Native grasses	Seeded grasses
One	77.78 (50.20) a	250.00 (81.35) b
Two	63.89 (29.10) a	372.22 (91.75) b
Three	66.60 (27.06) a	331.15 (81.68) b

Table 4: ANOVA results of the mean number of seeds per sample of seeded and native grasses in areas of different fire severity. N = 36.

Source	F	df	P
Model	9.90	5	<0.0001
Fire severity	5.90	2	0.0069
Grass type	21.58	1	<0.0001
Fire severity X grass type	10.20	2	0.0004

Table 5: Mean number of seeds per m^2 and standard error from native and seeded grasses in areas of low, moderate and high fire severity. N = 36. Different letters represent significant differences at the p<.05 level. Low severity areas were not aerially seeded.

Fire severity	Native grass seeds/m^2	Seeded grass seeds/m^2
High	11.00 (7.02) a	488.40 (124.20) b
Moderate	66.60 (58.63) a	579.42 (147.65) b
Low	114.78 (53.33) a	19.03 (9.90) a

Table 6: ANOVA results of mean number of native and seeded grasses in large plots ($1m^2$) in areas of low, moderate and high fire severity. N = 74.

Source	F	df	P
Model	10.01	5	<0.0001
Fire severity	1.28	2	0.2926
Grass type	6.28	1	0.0183
Fire severity X grass type	20.89	2	<0.0001

Table 7: Mean number of native and seeded grasses per m^2 and standard error in large plots (1m^2) in areas of low, moderate, and high fire severity. N = 74. Different letters represent significant differences at the $p<.05$ level. High and moderate severity areas received seeding treatment; low severity areas were not seeded.

Fire severity	Native grass plants/m^2	Seeded grass plants/m^2
High	0.17 (0.17) a	32.00 (7.67) b
Moderate	0.80 (0.49) a	17.60 (4.95) b
Low	22.17 (5.06) b	0.50 (0.34) a

Table 8: ANOVA results from mean seed density of native and seeded grass seeds from center soil samples in grass cover and bare ground plots. N = 74.

Source	F	df	p
Model	1.78	3	0.1593
Plot type	2.42	1	0.1245
Grass type	1.18	1	0.2806
Plot type X grass type	1.18	1	0.2806

Table 9: Mean density of native and seeded grass seeds per square meter and standard error in areas dominated by bare ground and native grass cover. N = 74. No estimates for density were significantly different at the $p<.05$ level.

Plot type	Native grass seed density	Seeded grass seed density
Grass cover	86.40 (45.70)	209.10 (69.00)
Bare ground	60.00 (46.6)	60.00 (41.00)

Table 10: Mean index of similarity (SI) and standard error for six different sampling intensities. One, two and three refers to the number of pooled soil samples for seed bank analysis, large refers to the 1 m^2 vegetation plot, and small refers to the 60 cm^2 plot. N = 168. There is no significant difference between treatments.

Number of soil samples	Vegetation Plot	Similarity Index
One	Small	0.12 (0.04)
One	Large	0.13 (0.04)
Two	Small	0.19 (0.05)
Two	Large	0.23 (0.05)
Three	Small	0.19 (0.05)
Three	Large	0.25 (0.05)

Table 11: ANOVA results for the effects of fire severity (high, moderate, and low), grass type (seeded and native) and their interaction on the index of similarity (SI). N=36

Source	F	df	p
Model	6.79	5	0.0002
Fire severity	1.75	2	0.1907
Grass type	22.94	1	<0.0001
Fire severity X grass type	5.59	2	0.0086

Table 12: Mean index of similarity (SI) and standard error between seed density and plant density for native and seeded grasses in areas of low, moderate and high fire severity. N = 36. Different letters represent significant differences at the p<.05 level.

Fire severity	Native grass SI	Seeded grass SI
High	0 (0) a	0.37 (0.06) bc
Moderate	0 (0) a	0.57 (0.05) b
Low	0.13 (0.08) a	0.17 (0.17) ac

CHAPTER 3: Impacts of exotic grasses used for post-fire erosion control on seedling recruitment of native grasses.

Abstract

In southwestern ponderosa pine forests, native perennial grasses perform important ecological functions. Thus, their recovery following severe wildfire is crucial yet often delayed because of high fire-induced mortality of plants and seeds. Application of seeds from exotic grasses or cultivars of native grasses (seeded grasses) and straw mulch for erosion control after a wildfire has the potential to further disrupt recovery of native grasses. In this study, I examined the effects of foliar cover of seeded grasses, straw mulch, litter, and seeded grass seed bank density on recruitment of native grasses seedlings. I showed that number of established native grass seedlings was negatively correlated with high cover of seeded grasses (-2.59 ± 1.45; 1 SE) and with cover of straw mulch (-4.25 ± 2.38; 1 SE). Seeded grass recruitment responded very differently to measured variables with positive correlations found between number of established seeded grass seedlings, and cover of litter (1.03 ± 0.36; 1 SE) and density of seeded grass seeds in the seed bank (1.05 ± 0.45; 1 SE). Results from the study show the potential for seeded grasses used in post-fire erosion control treatments to deter establishment of native grasses. The dominance of seeded grasses in this area seems likely to persist given

their high cover and the large number of seeds in the seed bank compared to native grasses.

Introduction

In systems adapted to frequent low intensity wildfire, uncharacteristically severe wildfire can result high mortality of understory plant species that are not adapted to high intensity fire (Armour et al. 1984; Vose and White 1991; Griffis et al. 2001). As a result, the understory of these burned areas is often dominated by exposed bare ground. Elimination of plants that act to stabilize soil can pose immediate threats to ecological communities and human life and property through resultant dramatic increases in runoff and soil erosion (DeBano et al. 1988). To mitigate such risks, managers often apply large amounts of grass seed to severely burned areas immediately after wildfire events in hopes of increasing vegetative cover. Often non-native grasses or native cultivars (seeded grasses) are used because of their wide availability, low cost, and ability to rapidly establish under a variety of conditions (Robichaud et al. 2000). It is assumed that seeded grasses will not persist in burned areas eventually allowing native plant species to reestablish (Beyers 2004). However, the same characteristics that allow seeded grasses to establish and grow rapidly may also allow them to competitively exclude native grasses. The effects of seeded grasses on native grass recovery are poorly understood in most systems. Further study is warranted given that in certain cases seeded grasses have resulted in lower native species diversity (Bock et al. 1986; Keeley 2004; Kruse et al. 2004) and limited reestablishment of native shrubs and trees (Griffin 1982; Elliot and White 1987; Amaranthus et al. 1993; O'Leary 1995; Schultz et al. 1955).

One factor that can affect the dominance of one or a few plant species at the expense of others is a species' differing capabilities for utilization of available resources such as water and nitrogen based on their evolutionary histories (Grime 1977; Chapin et al. 1986). Competitive exclusion can be particularly important at the seedling stage with established plants limiting available water and thus reducing survival of seedlings of other species (Hamilton et al. 1999). Strong competitive ability of established exotic grasses has shown to be a factor limiting recruitment of native grasses (Harris 1967; Brooks 2000; Humphrey and Schupp 2004). However, effective competitive exclusion of native grasses by exotic grasses often occurs only under certain environmental conditions (Corbin and D'Antonio 2004). Alternatively, cover of exotic grasses can provide shade and microsites suitable for establishment of certain plant species, particularly in post-fire environments (Smith et al. 2004).

Dominance of one species over another may also be a function of the number of seeds of either species that are present in a system with the species with more propagules often becoming the dominant species (Seabloom et al. 2003; Mouquet et al. 2004). Establishment of seedlings may be further enhanced if a particular species has the ability to germinate under a wide variety of conditions. One might expect cultivated grasses to germinate more readily than native grasses given that cultivars are often bred for rapid germination and establishment (Gustafson et al. 2004). Species may also respond differently to environmental factors such as shading, cover of pine litter, or cover of straw mulch used in post-fire erosion control efforts. The effects of pine litter and straw mulch may be very different as the mulch used in erosion control treatments tends to collect in rather thick layers (personal observation). Different levels of propagule supply and seedling establishment rates in a post-fire environment may play an important role in determining what grass species eventually dominates.

In this study, I examined the effects of percent cover (as a proxy for competitive effect and shading) of seeded grasses used for post-fire erosion control on recruitment by seed of native and seeded grasses. I also examined how other post-fire environmental factors such as cover of pine litter, and straw mulch influence establishment of native and seeded grasses. To determine how propagule pressure of seeded grasses might influence native and seeded grass establishment I examined the existing seed bank of seeded grasses and related it to density of native and seeded grass seedlings. Results should determine whether or not seeding with exotic grasses or native cultivars in post-fire rehabilitation treatments are detrimental or beneficial to native grass recovery.

Study site

This study was conducted at the Cerro Grande fire which burned 17,352 hectares in May of 2000 near the town of Los Alamos in northern New Mexico, USA (35° 52' N, 106° 19' W). The fire burned primarily through ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests. A few weeks after the fire all areas classified as high and moderate fire severity were aerially seeded with a mixture of four grass species at a rate of 600-seeds/m^2. Two of these species (*Hordeum vulgare* L. and *Lolium multiflorum* Lam.) are exotic annual grasses while the other two (*Bromus carinatus* Hook. & Arn. and *Elymus trachycaulus* (Link) Gould ex Shinners) are native perennial grasses. The two perennial grasses used however, while native to the state of New Mexico, are not common grass species in these ponderosa pine forests and were rare in the study area prior to the wildfire (Foxx 1994). Thus, I assume that the four species in the seed mix encountered in the study came from the seeding efforts rather than from individuals present prior to the wildfire. I made this distinction because cultivated varieties of native grasses are likely to respond differently to available resources than local varieties, as cultivated varieties are often bred for rapid germination, high seed production, or disease resistance (Gustafson et al. 2004), traits that could allow them to out-compete native local varieties. Here, I examined the effect of these four grasses on establishment of one native perennial grass, *Schizachyrium scoparium* (Mitchx.) Nash. *S. scoparium* is one of the most common native perennial grass species in ponderosa pine forests in the southwestern United States (Gould 1951) and thus, is a very important species in post-fire recovery. Many of the other dominant grasses in this forest type are perennial C_4 grasses and I assumed that their response to seeded grass cover would be similar to *S. scoparium*. Seeds of a local variety of *S. scoparium* were purchased from a commercial seed company and used in this study (Plants of the Southwest, Sante Fe, New Mexico, USA).

Methods

Three cover classes of seeded grasses were randomly assigned to 72 plots in an area that burned under high fire severity and was dominated by seeded grasses. The cover of seeded grasses was manipulated to conform to one of three cover classes; no cover, low cover (0-15%) and high cover (>15%). Removal experiments can have covarying effects with soil disturbance when plants are pulled from the ground (see D'Antonio et al. 1998 for discussion). To minimize soil disturbance, above ground plant parts were clipped below the root crown and removed from plots and root systems were left in tact.

In each plot percent cover of seeded grasses, native grasses, pine litter, and straw mulch was visually estimated after the cover of seeded grasses was manipulated. Straw mulch had been applied as part of erosion control efforts and was encountered on 8 of the plots. Litter cast from nearby trees was encountered on all plots. A soil sample was taken with a soil core (10 cm diameter, 5 cm depth) from the center of each plot for a seed bank analysis. Soil samples were sieved and searched for seeds from grasses in the aerial seed mix to estimate seed density in the seed bank. Seed from the seeded grasses were relatively large and easily detected through sieving soil. This method is not appropriate for detecting smaller native grass seeds, but I assumed that density of native grass seed would be very low based on a related soil seed bank study conducted near the study site (chapter 2). Cover manipulations were conducted in the spring of 2003. Approximately six g of *S. scoparium* seed (about 200 seeds) were then added to each plot in the spring of 2003. *S. scoparium* and similar C_4 grasses typically germinate in mid to late spring and their active growing season is throughout the summer (USDA, NRCS 2004). At the end of the growing season in the fall of 2003, the number of seedlings of native and seeded grasses was recorded in each plot. When the number of seedlings was greater than 100 per plot, seedlings density was estimated to the nearest 25. Percent cover of native and seeded grasses, litter and straw mulch was visually estimated in the spring of 2003, the fall of 2003 and the spring of 2004.

To assure that removal treatments resulted in reduced cover of seeded grasses that persisted over time, Analysis of Variance (ANOVA) was used to test for the effect of time (spring 2003, fall 2003, and spring 2004), cover class (0%, 0-15%, and >15%), and their interaction on cover of seeded grasses. Numerous variables that we measured had the potential to inhibit or enhance recruitment of native and seeded grass seed including seeded grass cover, cover of straw mulch, cover of pine litter, and density of seeded grass seeds in the seed bank. To determine the relative effects of each of these variables on number of native and seeded grass seedlings, multiple regression models were developed using different combinations of these predictor variables. I tested eleven using different combinations of predictor variables (Table 1). The same models were tested with number of native grass seedlings and number of seeded grass seedlings as the dependent variables. I selected the best model using an information theoretic approach (Burnham and Anderson 2002). Aikaike's information criterion (AIC) was calculated for each model based on the residual sum of squares (Burnham and Anderson 2002):

$$AIC = n\log(SSE/n) + 2K \quad \text{(Eq. 1)}$$

where n = sample size, SSE = sum of squares error, and K = number of parameters in the model. The model with the lowest AIC was considered to best fit to the data (best model). If other models showed considerable support (difference in AIC value from the best model less than 10) parameter estimates and associated standard errors from all appropriate models were averaged according to the procedures outlined in Burnham and Anderson (2002). Data were square-root transformed prior to analysis when the assumption of homogeneity of variance was not met. All statistical analysis was done using the SAS statistical package for Windows (version 9.1, SAS, 2002-2003, Cary, North Carolina, USA).

Results

In 2003 monthly precipitation was below the long-term average for May (3.4 cm), June (1.8 cm), July (0.7 cm) and August (7.1 cm) in the Los Alamos area. Monthly temperature was above the long-term average for May (14.4 °C), June (18.1 °C), July (23.2 °C) and August (19.8 °C) in the Los Alamos area in 2003.

Time, cover class and their interaction were significant effects in the ANOVA model examining these effects on seeded grass cover (Table 2). While cover of seeded grasses increased over time in each cover class treatment, differences in seeded grass cover among the three cover classes persisted over time with the highest cover class treatment exhibiting higher cover of seeded grasses than the low and no cover treatments (Figure 1). Thus, the relative effects of the different cover classes persisted throughout the study period.

Seedlings of native and seeded grasses established by the fall of 2003, however none of the seedlings survived by the spring of 2004. I suspect that the lower than average precipitation and higher than average temperature throughout the summer prevented the seedlings from reaching a size large enough to survive through the winter. Thus, the analysis presented in this study is for number of seedlings of native and seeded grasses in the fall of 2003. The range of seeded grass seeds found in the seed bank was 0 to 96 and the mean was 21.3 (± 2.1; 1 SE). When adjusted for the size of the plot (1-m^2), this results in approximately 2,100 seeds/m^2. This is much higher than the 200 seeds of *S. scoparium* added per plot and much higher than the average number of native grass seeds found in a related seed bank study (11.0 ± 7; 1 SE) (chapter 2). In an ANOVA comparing number of grass seedlings versus grass type (native or seeded), initial cover of seeded grasses (high, low, or none) and their interaction, the entire model was significant (F = 15.89, df = 5, n = 144, $p < 0.0001$). The significance was driven by the effect of grass type (F = 72.36, df = 1, $p < 0.0001$), as initial cover was not significant (F = 0.86, df = 2, p = 0.43). The interaction between grass type and initial cover class was nearly significant (F = 2.69, df = 2, p = 0.07). In all seeded grass cover classes, number of seeded grass seedlings was higher than that of native grass seedlings (Figure 2). Number of native grass seedlings appears to decrease as cover of seeded grasses increases, but differences between treatment means were not significant (Figure 2). Number of seeded grass seedlings significantly increases as cover of seeded grasses increases (Figure 2).

Eleven linear regression models with multiple variables were tested on number of seedlings of native and seeded grasses (Table 1). For number of native grass seedlings, the linear regression model which included cover of straw mulch only best fit the data, however there was a high degree of model selection uncertainty with no model showing a difference in AIC from the best model greater than 10 (Table 3). Since there was a high degree of model selection uncertainty in the models describing number of native grass seedlings, all models were considered in averaging parameter estimates and calculating associated standard errors. There were negative relationships between number of native grass seedlings and initial seeded grass cover and initial straw mulch cover (Table 4). There was high error associated with the parameter estimates for litter cover and number of seeded grass seeds in the seed bank and thus I could not conclude whether relationships between these variables and number of native grass seedlings were positive or negative.

The same eleven models were tested with number of seeded grass seedlings as the dependent variable. In this case the best model included percent litter cover and number of seeds from seeded grasses in the seed bank (Table 3). However, there was again a high degree of model selection uncertainty and thus all models were considered when estimating parameters and associated standard error values. There were positive relationships between number of seeded grass seedlings and all variables in the eleven tested models (Table 5). Cover of litter and number of seeds from seeded grasses in the seed bank seem to be drivers in these models as their estimates were associated with lower standard error values. There was high error associated with the parameter estimates for seeded grass cover and mulch cover thus I could not conclude whether relationships between these variable and number of seeded grass seedlings were positive or negative.

Discussion

Seeded grasses have high recruitment rates at the Cerro Grande fire. Seeded grasses persisted in this landscape up to four years after the fire and increased in cover in certain areas (chapter 4). This is likely to be a function of their competitive ability and the number of seeds in the study area. Seeded grasses were shown to have faster growth rates than native grasses in response to increasing nitrogen (chapter 4) and they dominate the seed bank (chapter 2). In this study the dominance of seeded grasses in the seed bank allowed high number of seeded grass seedlings regardless of other environmental factors such as foliar cover of seeded grasses and cover of straw mulch. Even though seedlings did not reach maturity, the overall increase in cover of seeded grasses over time and the high level of seedling recruitment suggests that seeded grasses will persist in this landscape and may dominate in certain areas.

Higher cover of seeded grasses reduced seedling recruitment of native grasses but not seeded grasses. The ANOVA model did not show significant effect of initial cover class on recruitment of native grass seedlings. However, in multiple linear regression models with seeded grass cover as a continuous predictor, percent cover of seeded grasses seems to be one factor that decreases recruitment of native grass seedlings. Cover of straw mulch used for erosion control also reduced recruitment of native grasses. No other studies have examined the impacts of straw mulch on native grass recruitment. Interestingly, seeded grass recruitment did not seem to be negatively impacted by the same environmental factors. Cover of seeded grasses and mulch had no discernable negative impact on seeded grass recruitment while cover pine litter and density of seeded grass seeds in the seed bank had positive impacts on seeded grass recruitment. These results suggest that seeded grasses are more likely to establish than native grasses in this post-fire environment where cover of seeded grasses remains high. If seeded grasses persist, they could delay recovery of native grasses by reducing recruitment success.

None of the seedlings of native grasses survived a year after planting thus the true effects of seeded grasses on establishment of native grasses cannot be concluded with the results of this study. However, the differences in number of established native grass seedlings in relation to our experimental treatments at the end of the first growing season suggest that seeded grasses have some impact on establishment of native grasses. At the Cerro Grande, areas that experienced high fire severity generally had reduced cover of native grasses and very low density of native grass seeds in the seed bank (chapter 2).

Thus, recruitment of native grasses from seed sources outside the fire area or from remnant grasses within the burned area is likely to be very important for native grass recovery following fire. In this study seedling establishment of native grasses was reduced by cover of seeded grasses. This could be partly because of the low propagule pressure of native grasses compared to seeded grasses. However, propagule pressure of seeded grasses seems less likely to be an important factor in native grass seeding recruitment, as I found the relationship between native grass seedlings and seed bank density of seeded grasses to be associated with high error values. This is similar to other studies which have found reduced recruitment of native grass by seed as a result of high cover of mature exotic grasses (Brooks 2000; Humphrey and Schupp 2004). Native grass recruitment also seems to be hampered by cover of straw mulch which is commonly used in post-fire rehabilitation efforts (Robichaud et al. 2000). Natural recovery of native grasses may be delayed if high cover of seeded grasses and straw mulch persists.

Dominance by seeded grasses may have very different ecological effects than dominance by native grasses. Grasslands dominated by seeded grasses have been shown to have lower species richness than grasslands dominated by native grasses (Bock et al. 1986). Seeded grasses can also competitively exclude tree and shrub seedlings more so than native species (Elliot and White 1987; O'Leary 1995). While post-fire rehabilitation treatments may reduce soil erosion in the short-term their long-term impacts on native species recovery should be considered when such treatments are used.

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Table 1: Multiple linear regression models tested on the number of seedlings of native and seeded grasses. All models are of the form $y = \beta_0 + x_1\beta_1 + \ldots. x_n\beta_n$ where n = the number of independent variables. Grass is cover of seeded grasses in the spring of 2003. Litter is percent litter cover in spring 2003. Seed bank is the number of seeds from seeded grasses found in seed bank analysis. Mulch is percent cover of straw mulch applied for erosion control efforts. N = 72 for each model.

Model	Independent variables
1	Grass
2	Litter
3	Seed bank
4	Mulch
5	Grass, litter
6	Grass, seed bank
7	Grass, mulch
8	Litter, seed bank
9	Litter, mulch
10	Seed bank, mulch
11	Grass, litter, seed bank, mulch

Table 2: ANOVA table for effects of time (June 2003, Sept. 2003, and June 2004), initial cover class (high, low, and none) and their interaction on foliar cover of seeded grasses. N = 216. Differences between treatment groups are statistically significant at the $p < 0.05$ level in each sampling time.

Source	df	*F*	p
Model	8	41.95	<0.0001
Error	207		
Time	2	32.39	<0.0001
Cover class	2	130.66	<0.0001
Time * cover class	4	2.38	0.0529

Table 3: Model selection results for eleven regression models tested on number of seeded and native grass seedlings in the fall of 2003. See table 1 for description of models. Delta (Δ) AIC is the difference between the best model (models 4 and 8) and every other model. Any model with ΔAIC less than 7 is considered to have sufficient support given the data (Burnham and Anderson 2002).

Dependent variable	Number of native grasses		Number of seeded grasses	
Model	AIC	ΔAIC	AIC	ΔAIC
1	209.216	0.006	269.426	3.368
2	210.219	1.008	266.189	0.132
3	210.677	1.466	267.439	1.381
4	209.211	0	268.817	2.759
5	211.187	1.976	268.115	2.057
6	211.238	2.028	269.092	3.035
7	210.110	0.899	270.277	4.219
8	212.222	3.012	266.057	0
9	211.385	2.174	268.347	2.289
10	211.026	1.816	268.757	2.699
11	214.210	4.999	270.467	4.410

Table 4: Parameter estimates (β_x) and standard error for four variables in models with number of native grass seedlings as dependent variable. Parameter estimates were averaged from eleven models.

Variable	Estimate	SE
Grass	-2.594	1.446
Litter	-0.159	0.225
Seed bank	0.121	0.185
Mulch	-4.248	2.377

Table 5: Parameter estimates (β_x) and standard error for four variables in models with number of seeded grass seedlings as dependent variable. Parameter estimates were averaged from eleven models.

Variable	Estimate	SE
Grass	0.646	0.688
Litter	1.030	0.362
Seed bank	1.052	0.450
Mulch	1.347	1.668

Figure 1: Change in percent foliar cover of seeded grasses over time in different initial cover classes (high, low, and none). N = 216. Differences between initial cover class groups are statistically significant at the $p<0.05$ level in each sampling time.

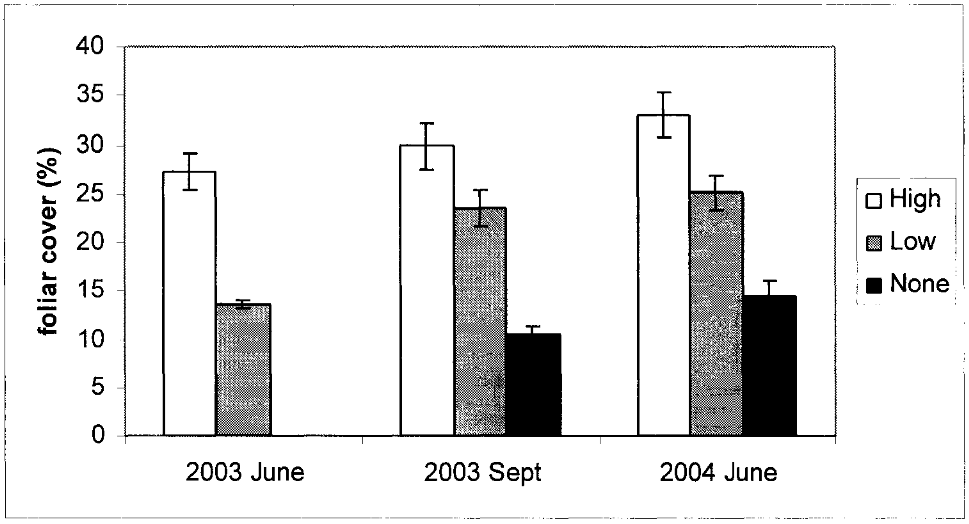
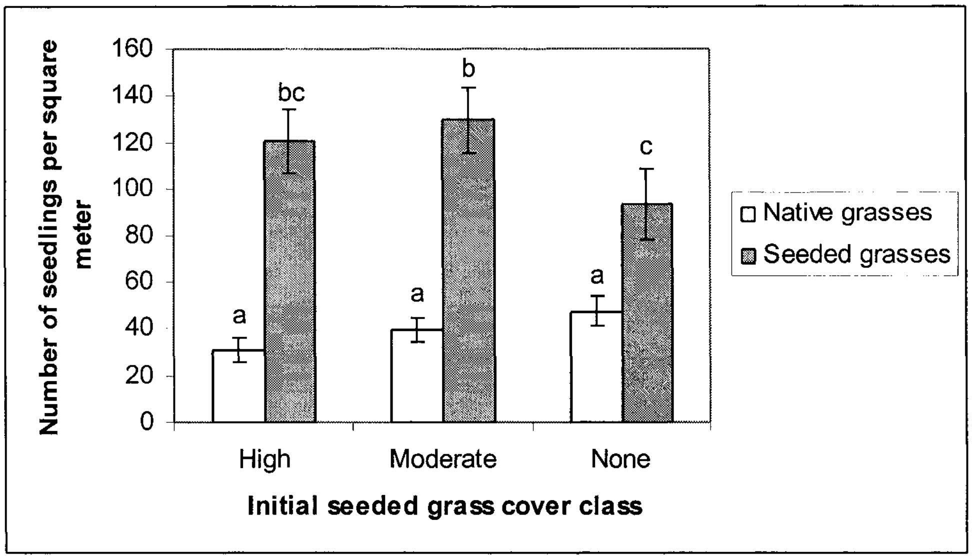


Figure 2: Mean number of native and seeded grass seedlings per square meter. Error bars represent standard error values. N = 144. Different letters represent significant differences at the $p < 0.05$ level.



CHAPTER 4: Response of native and cultivated grasses to availability of light and nitrogen in post-fire environments.

Abstract

Seeds from exotic or cultivated varieties of native grasses (seeded grasses) are often applied to areas burned in high severity wildfires to reduce the risks associated with increased fire-induced runoff and soil erosion. Such species may be undesirable ecologically if they out-compete native grasses, limit reestablishment of native trees and shrubs, and reduce native species richness, as they have shown to do in certain systems. In this study, I examined how native and seeded grasses respond to increasing availability of nitrogen and light in a greenhouse experiment to determine the potential for competitive dominance of seeded grasses. I then extrapolated the results of the greenhouse study to a burned landscape to determine if availability of light and nitrogen can be used to predict where native and seeded grasses are distributed across the landscape. In the burned area I examined relationships between native and seeded grasses to determine if seeded grasses may be out-competing native grasses in areas of high nutrient or light availability. I then examined how high cover of seeded grasses may influence overall native species richness.

In a greenhouse experiment, seeded grasses produced more biomass than native grasses when availability of nitrogen and light was high (*F* = 17.75, n = 330, df = 8, $p < 0.0001$). Across the burned landscape total nitrogen was found to be higher in mixed conifer forests compared to ponderosa pine forests and pinyon-juniper woodlands (*F* = 7.27, n = 25, df = 2, p = 0.003) and percent canopy cover was higher in mixed conifer forests compared to pinyon-juniper forests (*F* = 2.62, n = 26, df = 2, p = 0.10). Increased cover of seeded grasses from 2001 to 2004 occurred in mixed conifer forests where total nitrogen was higher (*F* = 18.08, n = 52, df = 4, $p < 0.0001$). Cover of native grasses increased from 2001 to 2004, especially in areas that burned with low fire severity (*F* = 3.25, n = 52, df = 2, p = 0.009). At the neighborhood scale (1-m^2), overall native species richness was negatively correlated with seeded grass cover (-0.133 $\pm$ 0.10; 1 SE) but positively correlated with native grass cover (0.505 $\pm$ 0.09; 1 SE). This effect was stronger in mixed conifer forests where cover of seeded grasses was higher. Effects of native and seeded grasses on native species richness became insignificant at the 1000-m^2 scale (*F* = 0.63, $r^2 = 0.08$, p = 0.61). In this study I show that seeded grasses do in fact persist in the burned landscape up to four years after a wildfire. On the landscape scale, the persistence of seeded grasses does not seem to impact native grass recovery or native species 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 forage for wildlife, nutrient retention, and soil stabilization (Cooper

1960; McPherson 1997). In these fire-adapted systems, grass production often increases after fire because of increased availability of resources such as light and nitrogen (White et al. 1991). However, an unusually severe wildfire can cause a delay in recovery of native grasses because of high mortality of individual grasses and seeds in the seed bank and reduction in seed rain (Armour et al. 1984; Vose and White 1987). Delay in native grass recovery leads to increased cover of exposed bare ground which may create opportunities for exotic species to establish (Keeley et al. 2003; Keeley 2004) and can increase the potential for harmful runoff and soil erosion (DeBano et al. 1988).

To mitigate the ecological risks associated with low post-fire native grass cover, areas that experience high fire severity are often aerially seeded with grass seed in hopes of rapidly establishing vegetation and reducing the cover of exposed bare ground. In such efforts, non-native grasses or cultivated varieties of native grasses (seeded grasses) are often used because of their wide availability, low cost, and ability to quickly establish (Robichaud et al. 2000). Despite their wide use, seeding treatments remain controversial because of their potential to reduce survival of tree seedlings (Elliot and White 1987; Barclay et al. 2004; Keeley 2004; Kruse et al. 2004), reduce native species richness (Bock et al. 1986; Brooks 2000; Humphrey and Schupp 2004; Keeley 2004), and introduce other exotic species through contamination of seed mixes (Kruse et al. 2004). Seeded grasses also have the potential to out-compete native grasses, limiting long-term recovery. However, the effects of seeded grasses on post-fire native grass recovery are poorly understood in many systems. In some cases, seeded grasses have been found to be poorly adapted to a particular site, persisting for only a couple years and then allowing native grasses to reestablish (Barclay et al. 2004). In another case, seeded grasses were found to be well-adapted to a site and thus able to persist and dominate, having negative impacts on native grass recovery and native species diversity (Bock et al. 1986)

Whether or not seeded grasses competitively exclude native grasses may be due to several factors including 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 and DeWald 1999; Abbot and Roundy 2003; Brooks 2003). Differing utilization strategies for resources can ultimately allow one species to out-compete another for available resources (Brooks 2003; Corbin and D'Antonio 2004; Humphrey and Schupp 2004). We might expect native and seeded grasses to respond differently to available resources, given that cultivated native and exotic grasses are adapted to high nutrient soils and are often bred for rapid germination, high seed production or rapid growth rate (Gustafson et al., 2004). Thus, we may expect cultivars to be better able to out-compete native grasses, particularly in areas with higher availability of resources such as light and nitrogen. This may be particularly important in the post-fire environment where we would expect an increase in resource availability. Nutrient availability should be particularly high in mid to high elevation forests (Gosz and White 1986) and in areas that burned under low or moderate fire severity (Raison 1979). Light availability should increase with fire severity.

In this study, I examined how seeded and native grasses responded to increasing availability of soil nitrogen and light. I hypothesized that seeded grasses would have higher growth rates than native grasses with higher nitrogen and light availability because the seeded grasses are cultivated varieties adapted to high nutrient conditions. I also examined if differing resource use could explain how seeded and native grasses were distributed across a burned landscape. I hypothesized that total nitrogen would be higher in higher elevation forests and in areas that burned with low fire severity. At similar elevations in the central Rocky Mountains, total nitrogen (from litter) was found to correlate strongly with annual net nitrogen mineralization which is a better indicator of plant available nitrogen (Stump and Binkley 1992). Thus, I expected seeded grasses to be higher in areas where total nitrogen was higher and I expected this to correspond to mixed conifer forests and areas that burned under low fire severity. Finally I examined if seeded grasses persist and spread up to four years post-fire and how this impacted recovery of native grasses and native plant species richness. Where cover of seeded grasses remains high, I expected there to be lower cover of native grasses and lower species richness.

Study site

This study was conducted at the Cerro Grande burn which occurred in May of 2000 near the town of Los Alamos in northern New Mexico, USA (35° 52' N, 106° 19' W). The fire burned 17,352 hectares in ponderosa pine (*Pinus ponderosa* P. & C. Lawson), mixed conifer (*P. ponderosa, Pseudotsuga menziesii* (Mirbel) Franco, *Pinus flexilis* James) and pinyon-juniper (*Pinus edulis* Engelm. and *Juniperus monosperma* (Engelm.) Sarg.) forest types. 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 Shinners, *Bromus carinatus* Hook. & Arn., *Hordeum vulgare* L., and *Lolium multiflorum* Lam. Two of the four grasses used in the reseeding efforts are annual grasses exotic to New Mexico (*L. multilforum* and *H. vulgare*). The other two seeded grasses are perennial and considered native to New Mexico (*E. trachycaulus* and *B. carinatus*). However, because these grasses are not common components of the forest types in the vicinity of the Cerro Grande fire and would not have been prevalent prior to the fire (Foxx 1994), I assumed that all individuals of these species encountered in the burned area were cultivated grasses that came from post-fire reseeding efforts. This assumption was strengthened by the fact that these grasses were not found in adjacent unburned areas.

Methods

Greenhouse Study

Seeds from seven grass species were collected from the Cerro Grande burn area in August of 2001. Four of the species had been seeded for purposes of erosion control after the fire (*E. trachycaulus, B. carinatus, H. vulgare,* and *L. multiflorum*). Three species were present in the study area before the fire. Two of these are common native perennial grasses (*Schizacyrium scoparium* (Michx.) Nash and *Koeleria macrantha* (Ledeb.) J.A. Schultes) and one is an exotic annual grass (*Bromus tectorum* L.). All grasses are classified as cool-season (C_3) except for *S. scoparium* which is a warm season (C_4) grass. All seeds were sown in flats filled with potting soil and placed in a heated greenhouse. Once seedlings established, they were transplanted into 10-cm diameter pots filled with sand and vermiculite mixed in a 1:1 ratio. Pots were watered daily and received four hours of supplementary artificial light per day.

A factorial experiment was designed to determine how the seven grass species respond to increased availability of light and nitrogen. Light treatments included full and partial sun. In the partial sun treatments, a black shade cloth excluded 63% of incoming light. Nitrogen treatments included low and high additions of nitrogen and a control. Nutrient solutions were made by mixing constant levels of micro- and macro-nutrients and differing levels of nitrogen in the form of ammonium nitrate (NH_4NO_3). 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 micro-nutrients only (no nitrogen). The values for total nitrogen received in the high and low nitrogen treatments were based on the range of annual nitrogen mineralization rates found in unburned forests near the study area (Gosz and White 1986). At the end of the experiment, above and below ground plant parts were harvested and placed in a drying oven at 75° C for three days. Total plant dry weight was then recorded for each plant.

Analysis of Variance (ANOVA) was used to test for differences in plant dry weight among species. Differences in dry weight were tested among seeded perennial and annual grass species and native perennial grass species. When no differences in dry weight were detected among species, plants from different species were combined and analyzed as functional groups (Table 1). I used ANOVA to test for the effect of light (high and low), nitrogen (high, low, and none) and functional group on dry weight. All analyses were done using the general linear model procedure (proc glm) in the SAS statistical program for Windows (version 9.1, SAS, 2002-2003, Cary, North Carolina).

Vegetation Assessment

In the summer of 2001, vegetation data were collected from within the perimeter of the Cerro Grande fire in Los Alamos, New Mexico. Plot locations were chosen in a stratified random manner by vegetation type (ponderosa pine, mixed conifer, and pinyon-juniper) and fire severity class (high and low). There were four plots per stratum except for the low severity pinyon-juniper strata which had two extra plots. In total, I sampled 26 plots. At each random location I established a modified-Whittaker plot (Stohlgren et al. 1995). Percent foliar cover of all species was measured in ten 1-m^2 subplots arranged within a 1000-m^2 plot. Cover of all abiotic features (soil, rock, litter, etc.) was also measured in the 1-m^2 subplots. Species richness was recorded in the 1000-m^2 plot, ten 1-m^2 subplots, two 10-m^2 subplots and one 100-m^2 subplot all nested within the 1000-m^2 plot. In the center of each plot I estimated percent canopy cover using a densiometer. Soil samples were taken from each corner and the center of the plot, pooled, and analyzed for total organic nitrogen and carbon. Fire severity was assessed at the 1-m^2 scale by estimating the downward heat pulse based on char ratings adapted from Ryan and Noste (1985). At the 1000-m^2 scale average char depth from the ten 1-m^2 subplots was used as an indicator of fire severity. Char depth is likely to be a better indicator of fire-induced understory plant mortality than other indicators of fire severity (i.e. percent crown consumption). I sampled vegetation in all plots again in the summer of 2004.

In this study, the experimental unit represents the randomized plot stratified by fire severity and vegetation type. Data on effects of grass type (native versus seeded) and year (2001 and 2004) were taken on the same experimental unit. This design is equivalent to a split-split-plot (Yandell 1997). The split-plot effect was year and the split-split-plot effect was grass type. To test the effects vegetation type and fire severity on cover of native and seeded grasses in both years, a split-split-plot ANOVA was conducted with percent foliar cover as the dependent variable and grass type (seeded and native), year (2001and 2004), vegetation type (mixed conifer, ponderosa pine, and pinyon-juniper) and fire severity (high and low) as independent variables. In this model, year, vegetation type, and fire severity were fixed effects and grass type X plot replicate nested within vegetation type and 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 procedure (proc mixed) in the SAS statistical program for Windows (version 9.1, SAS, 2002-2003, Cary, North Carolina).

Percentage of total nitrogen has been shown to vary by forest type (Gosz and White 1986) and fire severity (Raison 1979), thus I expected the same to be true in at the Cerro Grande fire. To verify that total nitrogen changes with fire severity and vegetation type, ANOVA was used to test for the effect of vegetation type, fire severity and their interaction on total nitrogen. The same model was used to test the effects of vegetation type and fire severity on percent canopy cover. A split-plot ANOVA was used to determine how cover of bare ground varied by fire severity, vegetation type, and year.

To test the effects of cover of native and seeded grasses and char depth on native species richness, I used multiple regression analysis. Multiple linear regression models were tested with native species richness as the dependent variable and char depth, native grass cover and seeded grass cover as dependent variables. I hypothesized that native and seeded grasses to have different effects on species richness as seeded grasses may out-compete other native species if they have higher growth rates. Models were tested for plots in different vegetation types, fire severity classes and years at the 1-m^2 and 1000-m^2 scales. Data from variables that showed non-normal distribution of residuals were square-root transformed prior to analysis.

Results

Greenhouse Study

Sample sizes between species groups were not equal because of mortality of certain grasses over the course of the experiment. Therefore, Type III sum of squares was used to assess significance of models. I found no significant difference in dry weight between the two native perennial grasses *S. scoparium* and *K. macrantha* ($F = 0.05$, n = 49, p = 0.82). There was a significant difference in plant dry weight among exotic annual grass species ($F = 4.89$, n = 96, df = 2, p = 0.01) with *L. multiflorum* having consistently greater dry weight than *B. tectorum* and *H. vulgare*. There was no significant difference in dry weight between *B. tectorum* and *H. vulgare* (p = 0.38). An ANOVA comparing dry weight of seeded perennial grasses (*B. carinatus* and *E. trachycaulus*) to *L. multiflorum* showed a difference in dry weight among species ($F = 3.75$, n = 95, df = 2, p = 0.03), again due mainly to a consistently greater dry weight of *L. multiflorum*. There was no significant difference in dry weight between *B. carinatus* and *E. trachycaulus* (p = 0.95). Based on these results I grouped grass species into four functional groups (Table 1) and used them for the remainder of the analysis.

In an ANOVA of dry weight by functional group, nitrogen treatment, light treatment, and their interactions, all variables in the model were significant (Table 2). All functional groups showed significantly higher dry weight with increasing availability of light and nitrogen (Figure 1). Native grass dry weight was consistently lower than dry weight for all other functional groups for all treatments except the control. Native grass biomass increased with increasing nitrogen levels only in the high light treatment. All other functional groups showed higher biomass with increasing nitrogen levels in both high and low light treatments. The magnitude of difference between native grasses and grasses in other functional groups was lower in the low nitrogen + shade treatment.

Vegetation Assessment

Across the fire landscape, total N varied by vegetation type ($F = 7.27$, n = 25, df = 2, p = 0.003), but not by fire severity ($F = 2.64$, n = 25, df = 1, p = 0.12) or the interaction between vegetation type and fire severity ($F = 1.36$, n = 25, df = 2, p = 0.28). However, total N tended to be higher in areas that burned under low fire severity (0.17 ± 0.04; 1 SE) compared to areas that burned under high fire severity (0.11 ± 0.02; 1 SE). Total N was highest on mixed conifer plots and lower on pinyon-juniper and ponderosa pine plots (Table 3). Percent canopy cover did not vary significantly by vegetation type ($F = 2.62$, n = 26, df = 2, p = 0.10), although it did appear substantially higher on mixed conifer plots compared to pinyon-juniper plots (Table 4). Canopy cover varied significantly by fire severity ($F = 5.98$, n = 26, df = 1, p = 0.02), but the interaction between fire severity and vegetation type was not significant ($F = 1.66$, n = 26, df = 2, p = 0.22). Percent canopy cover was significantly lower on high severity plots (25.24 ± 3.95; 1 SE) compared to low severity plots (41.17 ± 6.36; 1 SE). Cover of bare ground varied significantly by fire severity ($F = 27.95$, n = 52, df = 1, $p < 0.0001$), year ($F = 10.56$, n = 52, df = 1, p = 0.002), vegetation type ($F = 8.62$, n = 52, df = 2, p = 0.001) and the interaction between fire severity and year (F = 6.08, n = 52, df = 1, p = 0.018). The interaction between vegetation type and year was not significant (F = 1.18, n = 52, df = 2, p = 0.319). Cover of bare ground was highest in high severity plots in 2001 (Figure 2). By 2004 cover of bare ground had decreased in high severity plots to levels similar in low severity plots.

A split-split-plot ANOVA was conducted with percent foliar cover as the dependent variable and grass type (native versus seeded), vegetation type (mixed conifer, ponderosa pine, and pinyon-juniper), year (2001 and 2004), and fire severity class (high and low) as independent variables. Year, vegetation type, and fire severity were treated as fixed effects while plot replicate X grass type nested within vegetation type and fire severity was treated as a random effect. In this analysis all factors except for fire severity and vegetation type were significant (Table 5). The four-way interaction between grass type, vegetation type, fire severity and year was not significant and thus was dropped from the model.

Cover of seeded grasses did not change from 2001 to 2004 in either fire severity class (Figure 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 greater in areas of low fire severity compared to high fire severity while cover of seeded grasses was higher in areas of high fire severity compared to low fire severity.

The 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 (Figure 4). The 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. The 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. The cover of seeded grasses appears higher than cover of native grasses in mixed conifer stands in 2004 but the difference was not significant. The cover of native grasses increased from 2001 to 2004 in mixed conifer and ponderosa pine stands. The cover of native grasses was relatively high in 2001 in pinyon-juniper stands and remained constant in 2004.

Multiple regression analysis showed that effects of char depth, and seeded and native grass cover had little impact on native species richness at the plot (1000-m^2) scale (Table 6). Results varied when all plots were included in analysis versus plots from a single vegetation type or fire severity class. In most models there was a significant or nearly significant positive correlation between native species richness and native grass cover. There was a nearly significant negative correlation between seeded grass cover and native species richness in ponderosa pine plots in 2001 but a significant positive relationship between species richness and seeded grass cover in pinyon-juniper plots in 2004. In most cases, there was a positive correlation between native species richness and char depth, but a significant result was found only in low severity plots in 2004.

At the neighborhood (1-m^2) scale, many of the models show positive correlations between native species richness and native grass cover and negative correlations between native species richness and seeded grass cover (Table 7). The strongest negative correlation between native species richness and seeded grass cover occurred in mixed conifer forests in 2004. This may be due to the increase in cover of seeded grasses observed in these areas (Figure 4). When char depth was significant in models, a positive correlation between native species richness and char depth was found.

Discussion

Exotic and seeded grasses may have distinct competitive advantages in post-fire mixed conifer stands. Results from the greenhouse study showed that native perennial grasses respond differently to increasing availability of light and nitrogen than seeded and exotic grasses (Figure 1). Cultivated annual and perennial grasses produced more biomass with increasing availability of light and nitrogen compared to native grasses, especially in high nitrogen treatments. Based on ecological theory we might expect seeded and exotic grasses to be more likely to out-compete native grasses in areas with high nitrogen and/or light availability across the burned landscape (Chapin et al. 1986). This would be consistent with other studies that have shown that in systems with low soil fertility exotic grasses are better to produce more biomass and out-compete native grasses in areas with high nitrogen availability (Maron and Jeffries 1999; Brooks 2003; DeFalco et al. 2003). In our study system, total soil nitrogen was highest in mixed conifer stands and light availability was highest in pinyon-juniper stands and in areas that burned under high fire severity. Higher cover of seeded grasses in 2004 corresponded to mixed conifer stands where total nitrogen was higher. Conversely, native grasses recovered in 2001 in areas where total nitrogen levels were low (pinyon-juniper woodlands). This increase in cover of seeded grasses in mixed conifer stands from 2001 to 2004 seems likely to be a result of these grasses ability to capitalize on higher levels of total nitrogen.

How do native plant species persist in post-burn environments filled with potentially invasive species? While cover of seeded grasses increased or remained constant over time in certain areas, this did not seem to impact recovery of native grasses. From 2001 to 2004, cover of native grasses increased in all vegetation types and in areas of low fire severity. This indicates that native grasses are recovering in the burned areas despite high cover of seeded grasses. This may be consistent with studies that show that while competition is an important factor driving species interactions at neighborhood scales, at larger spatial scales other factors become larger drivers for species assemblages (Stohlgren 2002). However, given that this environment is still in the early stages of succession, competition may become a more important driver for species assemblages as succession proceeds. While seeded grasses have not prevented recovery of native grasses, it is unclear whether they will continue to expand in certain areas and if this will reduce cover of native grasses. Up to four years post fire, there is still high availability of bare ground, indicating the potential for seeded grasses to continue to spread in certain areas and this may have negative impacts on native grass establishment. In a related study, I found that high cover of seeded grasses reduced recruitment of native grasses from seed on a local scale (chapter 3)

Persistence of seeded grasses four years after the fire may have some negative consequences for native species richness. At the 1-m^2 scale native species richness was consistently negatively correlated with cover of seeded grasses. In contrast, native species richness was positively correlated with cover of native grasses indicating that seeded grasses have a very different ecological effect than native grasses. Other studies have shown that seeded grasses can have very different effects on native plant diversity than native grasses (Bock et al. 1986). Seeded grasses seem to have less of an effect on native species richness at the 1000-m^2 scale. This may change over time if seeded grasses continue to persist and increase in cover in certain areas beyond four years post-fire. At both scales, model r^2 values were relatively small, indicating that other variables not measured in this study are likely to be more important drivers for native species richness.

Post fire seeding treatments are controversial because some studies have shown that they are ineffective in reducing runoff and erosion (Robichaud et al. 2000; Wagenbrenner 2003) and because their potential negative impacts on tree recruitment (Elliot and White 1987), native species richness (Bock et al. 1986), and their potential for facilitating introductions of other exotic species (Kruse et al. 2004). While most treatments are applied with the intention that grasses will not persist, lack of persistence of seeded grasses has not been confirmed in most cases. In this study I showed that seeded grasses used for post-fire erosion control persist and expand in certain areas up to four years post-fire. I showed that this has some negative consequences for native plant species richness at small spatial scales. The high amount of exposed bare ground up to four years post-fire indicates the potential for seeded grasses to spread into open habitats. Based on results from this study, we might expect seeded grasses to expand in areas with high nutrient availability and this may influence of native grasses at small spatial scales (chapter 3). This is likely to further reduce species richness at the local scale since high cover of seeded grasses seems to reduce species richness while cover of native grasses seems to allow for occurrence of other native species. However, cover of seeded grasses is not likely to impact species richness at the landscape scale. I recommend that these potential ecological costs associated with post-fire seeding treatments be evaluated in decision-making processes regarding post-fire erosion control.

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Table 1: Functional groups used in analysis of data from greenhouse experiment on effects of light and nitrogen on grass dry weight. Rye grass is separated because of its consistently higher dry weight than other grass species.

Functional group	Species
Native perennial grasses	*Koeleria macrantha* and *Schizachyrium scoparium*
Exotic annual grasses	*Bromus tectorum* and *Hordeum vulgare*
Seeded perennial grasses	*Bromus carinatus* and *Elymus trachycaulus*
Annual rye grass	*Lolium multiflorum*

Table 2: ANOVA results from greenhouse experiment of the effect of functional group, nitrogen treatment, light treatment, and their interaction on grass dry weight (g). Functional groups are exotic annual grass, rye grass, native perennial grasses, and seeded perennial grasses. Nitrogen treatments are high nitrogen, low nitrogen and no nitrogen additions. Light treatments are full sun and shade. N = 303.

Source	F-value	df	P-value
Functional group	49.64	3	<0.0001
Nitrogen treatment	382.52	2	<0.0001
Light treatment	123.86	1	<0.0001
Functional group X nitrogen	22.89	6	<0.0001
Functional group X light	18.33	3	<0.0001
Functional group X nitrogen X light	17.75	8	<0.0001

Table 3: Mean percentage total soil nitrogen and standard error by vegetation type. Different letters represent significant differences at the $p < 0.05$ level. N = 25 (one missing value).

Vegetation type	Total N (%)
Mixed conifer	0.274 (0.07) a
Ponderosa pine	0.089 (0.01) b
Pinyon-juniper	0.098 (0.01) b

Table 4: Mean percent canopy cover and standard error by vegetation type. Different letters represent significant differences at the $p < 0.05$ level. $N = 26$.

Vegetation type	Canopy cover (%)
Mixed conifer	44.14 (7.88) a
Ponderosa pine	33.57 (2.75) ab
Pinyon-juniper	25.77 (7.92) b

Table 5: Results from split-split plot ANOVA with percent foliar cover as dependent variable and grass type, vegetation type, fire severity, and year as independent variables. Grass type X plot replicate is nested within fire severity class and vegetation type. N = 52.

Effect	Num df	F value	P value
Grass type	1	5.43	0.0245
Fire severity	1	0.15	0.7022
Year	1	15.50	0.0003
Vegetation type	2	2.90	0.0657
Grass X Fire	1	13.78	0.0006
Grass X Year	1	7.27	0.0099
Grass X Veg	2	5.21	0.0093
Grass X Fire X Year	2	3.25	0.0093
Grass X Veg X Year	4	18.08	<0.0001

Table 6: Multiple regression analysis of native species richness versus seeded grass cover, native grass cover and char depth at the 1000 m^2 scale for data collected in 2001 and 2004. All models where in the form of $y = \beta_0 + x_1\beta_1 + .. x_n\beta_n + \varepsilon$. Parameter estimates ($\beta_n$), associated standard error and p-values are given for each variable in each model. Analysis is for all plots, and plots within a vegetation type and fire severity class.

Variable	Estimate	SE	p	Estimate	SE	P
	2001			2004		
All plots	$F = 2.36$, p = 0.10, $r^2 = 0.24$			$F = 0.63$, p = 0.61, $r^2 = 0.08$		
Seeded grass cover	0.107	0.36	0.77	0.429	1.45	0.77
Native grass cover	0.631	0.24	0.02	-0.228	1.85	0.90
Mean char depth	2.297	2.24	0.32	1.733	2.86	0.55
Mixed conifer plots	$F = 0.49$, p = 0.71, $r^2 = 27$			$F = 0.89$, p = 0.52, $r^2 = 0.40$		
Seeded grass cover	-0.176	0.53	0.76	1.046	2.32	0.68
Native grass cover	1.677	1.81	0.41	8.507	6.01	0.23
Mean char depth	2.284	4.68	0.65	12.389	7.98	0.20
Ponderosa pine plots	$F = 1.29$, p = 0.39, $r^2 = 0.49$			$F = 2.69$, p = 0.18, $r^2 = 0.67$		
Seeded grass cover	-0.486	0.83	0.59	-5.753	2.83	0.11
Native grass cover	2.827	1.518	0.14	0.807	4.07	0.85
Mean char depth	6.065	5.644	0.34	11.140	5.28	0.10
Pinyon-juniper plots	$F = 5.55$, p = 0.04, $r^2 = 0.72$			$F = 0.26$, p = 0.85, $r^2 = 0.12$		
Seeded grass cover	1.198	0.48	0.05	2.310	4.25	0.61
Native grass cover	1.040	0.28	0.01	-1.172	2.43	0.65
Mean char depth	4.055	2.99	0.22	-4.648	5.48	0.43
High severity plots	$F = 1.73$, p = 0.24, $r^2 = 0.39$			$F = 0.37$, p = 0.78, $r^2 = 0.12$		
Seeded grass cover	-0.188	0.62	0.77	0.229	3.70	0.95
Native grass cover	0.534	0.36	0.17	4.551	6.67	0.51
Mean char depth	-5.491	5.67	0.36	9.417	9.19	0.34
Low severity plots	$F = 2.13$, p = 0.16, $r^2 = 0.39$			$F = 0.41$, p = 0.75, $r^2 = 0.11$		
Seeded grass cover	0.292	0.47	0.55	1.658	1.75	0.37
Native grass cover	1.102	0.44	0.03	-0.448	1.94	0.83
Mean char depth	14.241	7.54	0.09	-5.736	5.61	0.33

Table 7: Multiple regression analysis of native species richness versus seeded grass cover, native grass cover and char depth at the 1-m^2 scale for data collected in 2001 and 2004. All models where in the form of $y = \beta_0 + x_1\beta_1 + .. x_n\beta_n + \varepsilon$. Parameter estimates ($\beta_n$), associated standard error and p-values are given for each variable in each model. Analysis is for all plots, and plots within a vegetation type and fire severity class.

Variable	Estimate	SE	P	Estimate	SE	P
	2001			2004		
All plots	F=10.20, $p < 0.0001$, $r^2 = 0.11$			F = 13.62, $p < 0.0001$, $r^2 = 0.14$		
Seeded grass cover	0.071	0.13	0.58	-0.133	0.10	0.18
Native grass cover	0.548	0.12	<0.0001	0.505	0.09	<0.0001
Mean char depth	-0.102	0.18	0.56	0.642	0.18	0.0006
Mixed conifer plots	F = 1.08, $p = 0.36$, $r^2 = 0.05$			F = 4.88, $p = 0.004$, $r^2 = 0.16$		
Seeded grass cover	0.312	0.30	0.30	-0.523	0.17	0.004
Native grass cover	0.280	0.70	0.69	0.381	0.24	0.12
Mean char depth	-0.686	0.50	0.17	0.642	0.67	0.34
Ponderosa pine plots	F = 3.49, $p = 0.02$, $r^2 = 0.12$			F = 8.68, $p < 0.0001$, $r^2 = 0.26$		
Seeded grass cover	-0.187	0.23	0.41	0.056	0.16	0.72
Native grass cover	0.671	0.34	0.05	0.531	0.11	<0.0001
Mean char depth	-0.188	0.25	0.46	0.014	0.20	0.94
Pinyon-juniper plots	F = 7.37, $p = 0.0002$, $r^2 = 0.19$			F = 13.74, $p < 0.0001$, $r^2 = 0.30$		
Seeded grass cover	0.166	0.19	0.38	-0.010	0.18	0.96
Native grass cover	0.609	0.14	<0.0001	0.554	0.09	<0.0001
Mean char depth	-0.106	0.28	0.71	0.446	0.21	0.03
High severity plots	F = 1.19, $p = 0.32$, $r^2 = 0.03$			F = 6.91, $p = 0.0003$, $r^2 = 0.15$		
Seeded grass cover	0.134	0.17	0.44	-0.199	0.14	0.16
Native grass cover	0.250	0.22	0.25	0.611	0.16	0.0003
Mean char depth	-0.155	0.30	0.61	0.356	0.35	0.31
Low severity plots	F = 7.45, $p = 0.0001$, $r^2 = 0.14$			F = 8.94, $p < 0.0001$, $r^2 = 0.17$		
Seeded grass cover	0.078	0.19	0.67	-0.124	0.14	0.39
Native grass cover	0.689	0.15	<0.0001	0.461	0.108	<0.0001
Mean char depth	1.070	0.39	0.01	1.321	0.40	0.001

Figure 1: Mean dry weight for grasses from greenhouse experiment in each functional group and each light and nitrogen treatment. Black bars represent native perennial grasses, grey bars represent seeded perennial grasses, white bars represent exotic annual grasses, and hatched bars represent rye grass. Different small case letters represent significant differences between means of different functional groups within each treatment group at the $p < .05$ level. Different upper case letters represent significant differences between means of different treatment groups within each functional group at the $p < 0.05$ level. Error bars represent standard error. N = 303.

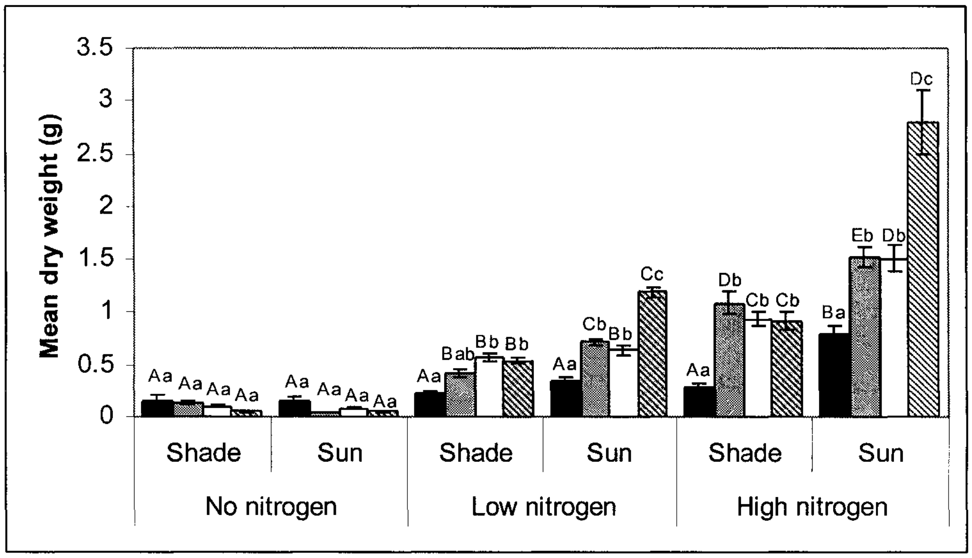


Figure 2: Mean percent cover of bare ground by fire severity class and year. Different letters represent significant differences at the $p < 0.05$ level. Error bars represent standard error. N = 30 for low severity groups N = 22 for high severity groups.

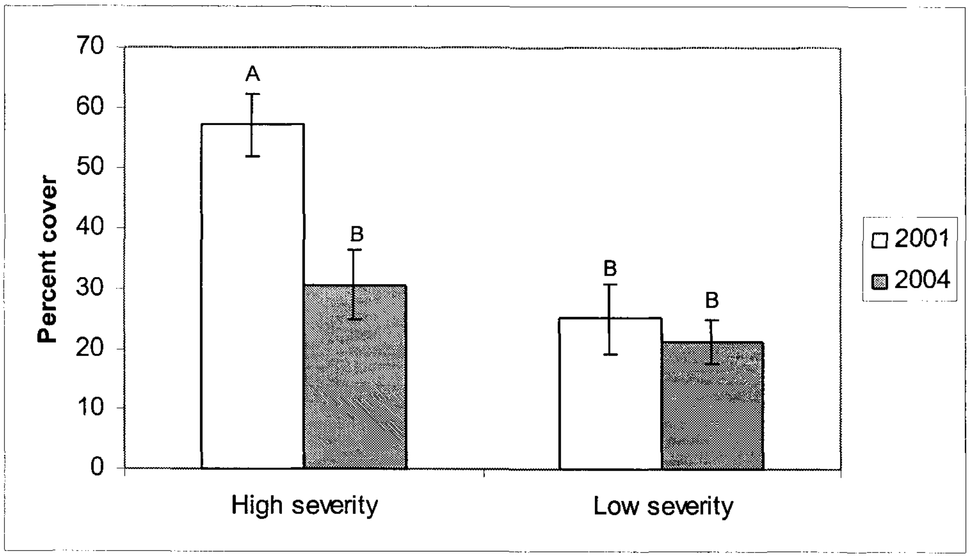


Figure 3: Mean percent cover of native and seeded grasses by fire severity class and year. Different lower case letters represent significant differences for native or seeded grasses between year and fire severity groups at the $p < 0.05$ level. Different upper case letters represent significant differences 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.

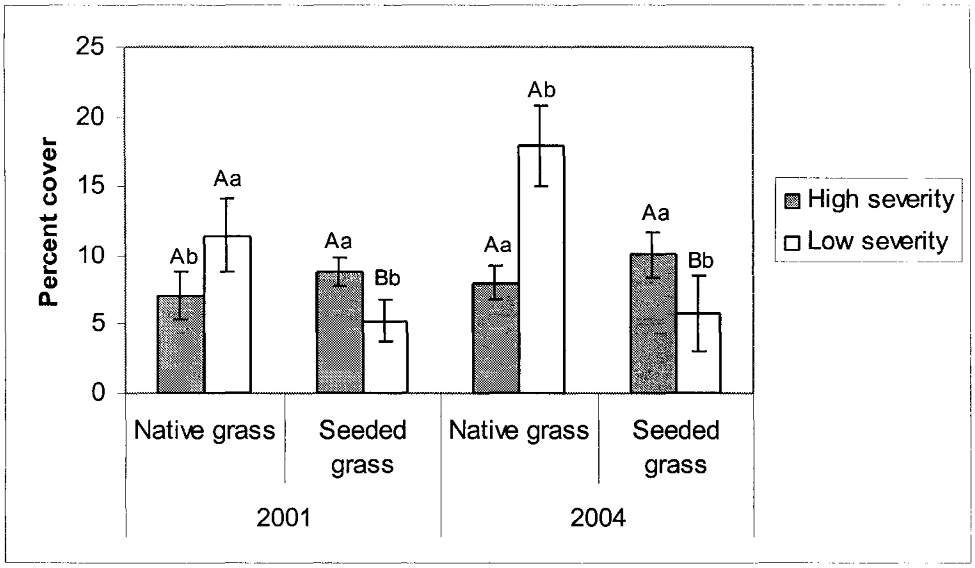
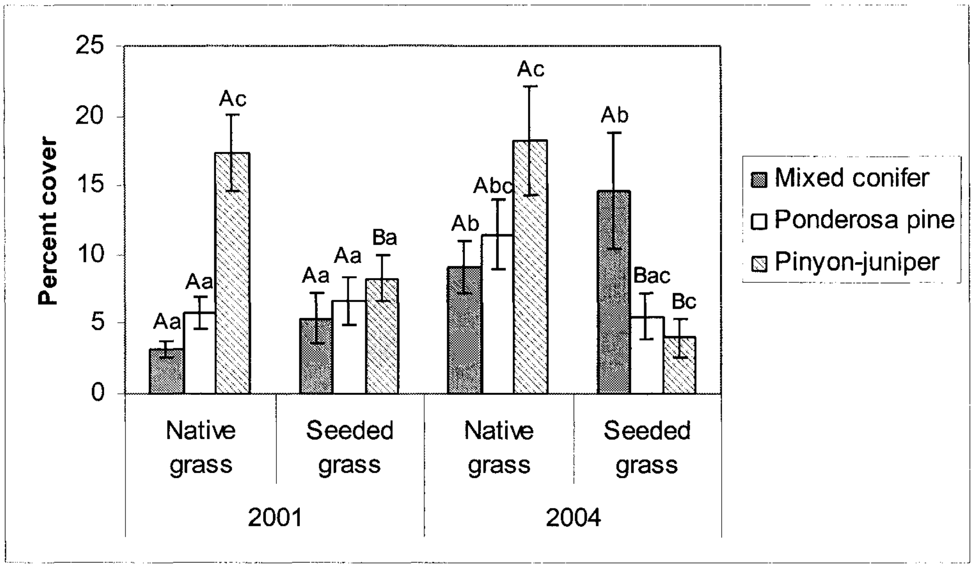


Figure 4: Mean percent cover of native and seeded grasses for different vegetation types in each year. Different lower case letters represent significant differences for native or seeded grasses between year and vegetation type groups at the $p < 0.05$ level. Different upper case letters represent significant 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. Error bars represent standard error. N = 10 for pinyon-juniper groups.



CHAPTER 5: Invasion of exotic plant species after wildfire: effects of abiotic and biotic factors and post-fire grass seeding treatments

Abstract

Exotic plants pose many threats to ecosystems, leading many researchers to attempt to determine where on landscapes exotic species are most likely to establish. Exotic species tend to be more common after disturbance, in areas of high nutrient availability, and when their supply of propagules is high. These characteristics can be used to describe forested areas that recently experience high severity wildfire and thus, establishment of exotic plant species after wildfires is a common concern because of the higher availability of resources and low cover of dominant native grass species. Application of grass seed mixes for post-fire erosion control may further facilitate establishment of exotic plant species if mixes are contaminated with seed from exotic species. Alternatively, application of grass seed may deter establishment of exotic plant species by rapidly establishing vegetation and reducing exposed bare ground. In this study I examined where exotic plant species establish one and four years after a wildfire in northern New Mexico in relation to various biotic and abiotic environmental factors. The abiotic factors included variables that have been shown to be good predictors of

exotic species cover (i.e., nitrogen availability, fire severity, canopy cover). The biotic factors included native species richness, native grass cover and seeded grass cover.

Exotic species cover was positively correlated with char depth, which is a proxy for fire severity (estimate = 5.20 ± 2.8; 1 SE). This was the only abiotic variable that was a consistent predictor for exotic species cover in both years and at two scales of measurement (1-m^2 and 1,000-m^2). At the 1,000-m^2 scale, exotic species cover was positively correlated with native species richness (estimate = 0.16 ± 0.06; 1SE) and seeded grass cover (estimate = 0.12 ± 0.08), and consistently negatively correlated with native grass cover (estimate = -0.75 ± 0.57; 1 SE). Similar trends were found at the 1-m^2 scale. I suspect that native grasses are able to deter establishment of exotic species when their cover is high. The positive correlation between exotic species cover and seeded grass cover is likely a result of contamination of the seed mixed used in the post-fire rehabilitation treatment with seeds from other exotic species. With this study I document the potential negative consequences of applying grass seed for erosion control treatments after wildfires. If such treatments are justified in a given case, more rigorous standards for testing seed mixes for purity should be implemented.

Introduction

Exotic plant species can pose serious threats to ecosystem structure and function by reducing native plant diversity (Knapp 1996; Christian and Wilson 1999; Alvarez and Cushman 2002), altering nutrient cycles, (Evans et al. 2001; Mack et al. 2001) and increasing fuel flammability (D'Antonio and Vitousek 1992). Since control of exotic species has proven difficult in many areas, researchers have sought to understand what determines community invasibility and traits of successful invaders in hopes of preventing the establishment and spread of exotic plant species. Research has found that exotic species are often much more likely to establish after a disturbance, particularly a disturbance of high severity (Hobbs and Huenneke, 1992; Stylinski and Allen 1999). Exotic species are often adapted to high nutrient environments, and thus, have higher growth rates in response to increasing nitrogen than native species adapted to low nutrient environments (Maron and Jefferies 1999; Brooks 2003; DeFalco et al. 2003). Thus, exotic species are often able to out-compete native species when nitrogen availability is high and they are often more likely to be found in areas with high resource availability across the landscape (Stohlgren et al. 1998). Exotic plant species also are more likely to establish when their supply of propagules is higher than that of native species (D'Antonio et al. 2001; Levine 2001).

Wildfires have long been a significant disturbance in the southwestern United States (Swetnam and Baisan 1996). Due to management practices in the 19th and 20th centuries, forest structure has been dramatically altered resulting in increased fuel loads, and thus, the potential for uncharacteristically large and intense wildfires (Covington and Moore 1994; Fule et al. 1997). These disturbances create ample opportunities for establishment of exotic plant species given their creation of large expanses of exposed bare ground and increased availability of resources such as light and nitrogen (DeBano et al. 1988) and increase in exotic species cover is often found after wildfires (Crawford et al. 2001; Keeley et al. 2003). Propagule pressure of exotic species may also be increased through increased movement of people and equipment associated with fire-fighting efforts into burned areas. Spread of exotic species after wildfires might best be discouraged through rapid detection and control before populations spread. However, reconnaissance of burned for newly established exotic species becomes increasingly difficult as wildfires become larger in size and more area needs to be searched. Detection of exotic plants would be more effective if one could predict where exotics are most likely to establish based on environmental characteristics. Several characteristics such as elevation, soil nitrogen content, and disturbance severity have been shown to be good predictors of exotic species establishment and they are likely to be good predictors in burned areas as well (Hobbs and Huenneke 1992; Stohlgren et al. 1999b; Keeley et al. 2003; Stohlgren et al. 1999b).

Biotic factors such as native species richness and cover of dominant species have also been shown to be good predictors of successful establishment of exotic species, especially at smaller scales (Tilman 1999; Smith et al. 2004). These factors may be particularly important for managers because they are often easier to manipulate than abiotic environmental factors. Experimental studies have reported both positive (Naeem et al. 2000) and negative (Robinson et al. 1995) relationships between exotic species establishment and native species richness at small scales. However, at larger scales and in natural settings it is more common to find positive relationships between exotic species richness and native species richness (Stohlgren et al. 1998). This dichotomy has been partly explained by scale, native species persistence, and by the significance of dominant native species rather than sub-dominant native species on invasibility of communities (Smith and Knapp 1999; Prieur-Richard et al. 2002). Dominant species tend to produce more biomass, and thus, may decrease establishment of other native and exotic species by preemptive use of space or other resources, thereby reducing both native and exotic species richness (Robinson et al 1995). Alternatively, more diverse communities may contain species from different functional groups able to extract resources from different niches in the same community, leaving fewer available niches for exotic plants to establish at very local scales (Naeem et al. 2000). At larger spatial scales, areas that have higher availability of resources such as light and nitrogen, tend to also support higher native species richness (Stohlgren et al. 1998). Exotic plant species also tend to favor high resource environments, leading to positive correlations between exotic and native species richness at larger scales (Stohlgren et al. 1999b). In our study system, the Jemez Mountains of New Mexico, perennial grasses tend to dominate the understory and contribute less to species diversity than sub-dominant forb species (Foxx 1994). If dominant native grasses produce enough biomass to deter establishment of exotic species and sub-dominant native species, we would expect exotic species cover to be negatively correlated with native perennial grass cover and positively correlated with total (forb, grass and shrub) native species richness.

The high cover of bare ground after wildfires presents opportunities for establishment of exotic species, increased runoff, and erosion. To mitigate such risks, managers often apply large amounts of grass seed to recently burned areas in hopes of rapidly establishing vegetative cover (Robichaud et al. 2000). One might expect seeded grasses to reduce successful establishment of exotic species, given that such treatments often result in high cover of seeded grasses in an areas where cover of bare ground would otherwise dominate (Barclay et al. 2004). In fact, this is often one of the justifications for application of grass seed after fires (Beyers 2004). However, these treatments also have the potential to increase the likelihood that exotic plants will establish. While seed mixes used for post-fire erosion control are tested for contamination of other exotic species, presence of a small percentage (variable by state) of noxious or undesirable plant seed is considered acceptable by law (USDA, Federal seed act 2004). This amount may be insignificant when seed is applied over small areas. However, when large amounts of seed (e.g., 45 kg) are applied over large areas (e.g., 15,000 hectares) the small percentage of exotic species present in the seed mix may increase the propagule pressure enough to establish populations across the burned landscape. Furthermore, seed mixes often are only tested for species that are included in the state noxious weed list. Often, these lists do not include certain plant species that are likely to pose serious threats to ecological integrity. For example, cheatgrass (*Bromus tectorum* L.) is not considered a noxious weed in many states (USDA, Federal seed act 2004), and thus, is not considered in seed purity tests even though it has been shown to significantly alter ecosystem function and reduce native plant richness in certain ecosystems (Knapp 1996).

The purpose of this study was to examine biotic and abiotic environmental factors that best predict where exotic plants are likely to establish after a wildfire in hopes of aiding managers in focusing eradication efforts. Abiotic factors included variables that have been shown be good predictors for exotic species establishment (i.e. nitrogen, fire severity, elevation). I also examined the relationships between cover of exotic species, native grasses, seeded grasses, and native species richness to determine how biotic variables may best be altered to deter establishment and spread of exotic plants. I expected exotic species to be positively correlated with native species richness and negatively correlated with native grass cover (dominant species cover). I expected exotic species to be positively correlated with cover of seeded grasses due to contamination of grass seed mixes. I also examined how exotic plant species spread over time. Based on results from other studies (Keeley et al. 2003) we would expect cover of exotics to increase over time in areas where they are initially found one year after the fire. Finally, I examined if environmental and biotic predictors for exotic plant cover were consistent up to four years post-fire.

Study Site

This study was conducted at the Cerro Grande fire in the Jemez Mountains in northern New Mexico, USA (35° 52' N, 106° 19' W). The Cerro Grande Fire burned approximately 17,000 ha in May, 2000. The fire burned over multiple vegetation types. One month after the fire, all areas of high and moderate fire severity (about 7,000 ha) were aerially seeded with a mixture of annual and perennial grasses. This seeding included two exotic annual species and two native perennial species (Table 1). The native perennial species are considered native to the state of New Mexico, but are not typically found in the understory of forests in the Jemez Mountains. Based on the observations of local land managers and vegetation studies in adjacent areas (Foxx, 1996), I assumed presence of seeded grasses was insignificant prior to the fire and thus all individuals from the seed mix encountered in the study were from post-fire reseeding efforts. In addition, I found no grasses used in the seed mix in adjacent unburned areas.

Methods

Using a stratified random sampling design, I established plots for monitoring vegetation in the summer of 2001, one year post-fire. The strata of interest included vegetation type (ponderosa pine forests, mixed-conifer forests, and pinyon-juniper woodlands) and fire severity (low, high, and unburned). In each stratum, I established at least four modified-Whittaker plots. The modified-Whittaker plot consists of one 100-m^2 plot, two 10-m^2 plots and ten 1-m^2 plots nested within a 1000-m^2 area (Stohlgren et al. 1995). Percent foliar cover and average height of all species in the 1-m^2 subplots was recorded. Species presence was then measured in each 10-m^2, the 100-m^2, and the 1000-m^2 plots. Thirty-four modified-Whittaker plots were established within and adjacent to the burned area. I assessed fire severity at the 1-m^2 scale using ground char classes developed by Ryan and Noste (1983). This has been shown to be appropriate for describing potential fire effects on understory species (Ryan and Noste 1983). The ground char ratings from the ten 1-m^2 subplots were averaged for each plot to estimate fire severity at the 1000-m^2 scale. I collected soil samples from the four outside corners and the center of each plot, pooled them, and then analyzed them for soil texture (% sand, % silt, and % clay), total soil carbon (%) and total soil nitrogen (%). Percent slope, absolute aspect, and elevation were also measured at each plot. In the center of each plot I measured canopy cover using a densiometer. Slope and absolute aspect were used to assess potential annual direct incident radiation (McCune and Keon 2002). Vegetation measurements were taken on all plots again in June 2004. Abiotic measurements were not taken in 2004 as I expected them to be relatively constant over four years.

Data Analysis

Analysis of variance (ANOVA) was used to determine if and where exotic plants increased in cover over time. The model included cover of exotic species as the dependent variable and vegetation type (mixed conifer forests, ponderosa pine forests, and pinyon-juniper woodlands), fire severity (high, low, and unburned) and their interaction as independent variables. Because samples sizes in treatment groups were unequal, type III sums of squares was used to assess significance. Analysis was done utilizing the general linear model procedure (proc glm) in the SAS statistical program for Windows (version 9.1, SAS, 2002-2003, Cary, North Carolina, USA).

Multiple linear regression models were developed to determine factors that would best predict percent cover of exotic species across the landscape. Model selection based on information theory is a useful approach to data analysis. Unlike other selection methods (i.e. forward or stepwise), the information theoretic approach optimizes precision by posing penalties for increasing bias through addition of parameter estimates to the model (Burnham and Anderson 2002). This technique also emphasizes a priori model construction based on hypotheses of interest. I chose a linear regression structure (with intercept) for all models for both the 1000-m^2 and 1-m^2 scale. Separate but consistent analyses were conducted for plots in 2001 and 2004. Variables were log or square root transformed prior to analysis to correct for non-normal distribution of error.

In developing the models, I was concerned with testing hypothesized correlations between the cover of exotic species, seeded grasses, native grasses and native species richness (positive or negative) and where on the landscape these relationships may be important relative to other abiotic factors. Thus, abiotic factors (incident radiation, total soil nitrogen, percent clay content, elevation, canopy coverage, and average char depth) were tested along with biotic factors (seeded grass cover, native species richness, and native grass cover). In developing models, abiotic characteristics were separated by those that are likely to be a direct result of the wildfire (total soil nitrogen, canopy coverage, and average char depth) versus those that are likely to vary as a result of some other environmental characteristic (elevation, percent clay content, and incident radiation). Separating these effects allowed me to determine if exotic species cover was best predicted by biotic factors, results from wildfire, other environmental variables, and if the same effects were important one and four years post-fire. In multiple regression models, biotic variables were then combined with abiotic variables related to the wildfire and other abiotic variables to determine the relative importance of the different categories of variables (biotic, fire abiotic, and other abiotic) in predicting exotic species cover. Seven multiple linear regression models were tested for plots at the 1000-m^2 scale (Table 2). Cover of exotic species was used as the dependent variable. I hypothesized positive relationships between exotic species cover and native species richness, seeded grass cover, soil nitrogen, clay, radiation, and char depth. I hypothesized negative relationships between exotic species cover and native grass cover. It is possible that dominance of native or seeded grasses one year after fire influences cover of exotic species four years after fire through initial facilitation or exclusion of exotic species establishment immediately after the fire. Thus, in 2004, I also tested the effects of the cover of native and seeded grasses and exotic species in 2001 on the cover of exotic species in 2004. Thus, eleven models were tested for the cover of exotic species in 2004 (Table 3). Data were analyzed using the general linear model procedure (proc glm) in the SAS statistical package for Windows (version 9.1, SAS, 2002-2003, Cary, North Carolina, USA). Akaike's Information Criterion (AIC) was calculated from the residual sum of squares error for each model (Burnham and Anderson 2002):

$$\mathrm{AIC} = n\log(\mathrm{SSE}/n) + 2K \quad \text{(Eq. 1)}$$

where n = sample size, SSE = residual sum of squares error, K = number of parameters. I then calculated AICc, which is a variation of AIC with an adjustment for small sample sizes (Burnham and Anderson 2002).

One might expect the biotic interactions (competition/facilitation) between exotic species, seeded grasses, and native grasses to be most important at the neighborhood scale (1-m^2) as this is the scale at which plant-plant interactions should be important. Thus, I assessed the relationships between cover of exotic species, seeded grasses, native grasses, and native species richness in the 1-m^2 plots. All abiotic variables except char depth were measured at the 1000-m^2 scale, and could not be used as continuous predictors in regression models at the 1-m^2 scale without violating assumptions of independence. Thus, I separated subplots by vegetation type (mixed conifer, ponderosa pine, and pinyon-juniper) and aspect (north and south) and used these as categorical predictors in Analysis of Covariance (ANCOVA) models. Percent cover of exotic species was the dependent variable for all models. Six ANCOVA models were tested for exotic species cover in 2001 (Table 4) and eleven models were tested for exotic species cover in 2004 (Table 5).

The strength of evidence in support of given models was assessed using AICc values. AICc were calculated from the sum of squares term which was found for each model using the general linear model procedure (proc glm) in the SAS statistical package for Windows (version 9.1, SAS, 2002-2003, Cary, North Carolina, USA). The model with the lowest AICc is considered to have the most support based on the data (best model). For each model, differences in AICc values from the best model (ΔAICc) were calculated. Models with ΔAICc ≥ 10 were considered to have no support based on the data, models with ΔAICc ≤ 3 were considered to show considerable support by the data, and models with $3 <$ ΔAICc < 10 were considered to show less support by the data but were not disregarded (Burnham and Anderson 2002). A weight was calculated for each model that is a measure of evidence for a given model being the best model in the set of possible models. The weight is calculated from the ΔAICc and varies between 0 and 1 with 1 indicating the highest support for a given model. When many models have relatively high weights (> 0.1) and low ΔAICc (< 10), considerable model selection uncertainty exists, meaning one cannot be overly confident that the selected best model (model with the lowest AICc) is in fact the model with the most support given the data. In such cases, parameter estimates from models with AICc less than 10 were averaged and a standard error for each parameter estimate was calculated based on the variability and the model weight. The procedures for averaging parameter estimates and calculating associated standard errors are outlined in Burnham and Anderson (2002).

Results

In the ANOVA of exotic species cover versus vegetation type, fire severity, year and their interaction, all variables were significant (Table 6). Overall cover of exotic species increased from 2001 to 2004 but increases in cover were not seen across the entire burned landscape (Figure 1). Cover of exotic species increased only in ponderosa pine areas of high fire severity. Exotic species cover also appeared to increase in pinyon-juniper areas, but differences between 2001 and 2004 were only significant for unburned areas. There was no increase in exotic species cover in mixed conifer plots regardless of fire severity.

The model that best fit for cover of exotic species at the 1000-m^2 scale in 2001 included all variables (Table 7). Because there was considerable support for two other models (models 4 and 6), parameter estimates from all three models were averaged and the resulting parameter estimates and associated standard errors can be seen in table 8. Certain parameter estimates proved more important in the models by being associated with lower standard error values. The most significant parameters for predicting exotic species cover included average char depth, native species richness, seeded grass cover, native grass cover, nitrogen content and clay content. Across the landscape I found positive associations between exotic species cover and char depth, native species richness, seeded grass cover and clay content. Exotic species cover tended to have negative associations with other variables such as native grass cover and nitrogen content.

The model that best fit cover of exotic species at the 1000-m^2 scale in 2004 included incident radiation, elevation, clay content, native species richness in 2004, native grass cover in 2004, and seeded grass cover in 2004 (Table 9). Because there was considerable support for other models (models 1, 2, 3, 6, 7, 9, 10, and 11), parameter estimates from the nine models were averaged and the resulting parameter estimates and associated standard errors can be seen in table 10. Similar parameter estimates were important predictors for exotic species cover in 2004. Exotic species cover tended to be positively correlated with depth, native species richness in (2001 and 2004), exotic species cover in 2001, and seeded grass cover in 2004. Exotic species cover tended to be negatively correlated with elevation and native grass cover (2001 and 2004).

The model that best fit cover of exotic species at the 1-m^2 scale in 2001 included seeded grass cover, native grass cover, and native species richness (Table 11). Because there was considerable support for other models (models 4 and 5), parameter estimates from the three models were averaged and the resulting parameter estimates and associated standard errors can be seen in table 12. Biotic variables proved to be very important at the 1-m^2 scale with exotic species cover showing positive relationships with native species richness and negatively relationships with native grass cover.

The model that best fit cover of exotic species at the 1-m^2 scale in 2004 included vegetation type, aspect, cover of bare ground in 2004, seeded grass cover in 2004, native species richness in 2004, and native grass cover in 2004 (Table 13). Because there were two other models that showed considerable support (models 7 and 10), parameter estimates from the three models were averaged and the resulting parameter estimates and associated standard errors can be seen in table 14. Again, biotic relationships appear to be very important at the 1-m^2 scale with exotic species cover exhibiting a positive correlation with seeded grass cover (2001 and 2004) and a negative correlation with native grass cover (2001 and 2004). Disturbance severity also proved to be important with exotic species cover showing a negative correlation with char depth.

Discussion

Researchers who have examined where exotics establish on a landscape scale have found many environmental characteristics that make consistent predictors such as soil fertility, elevation, and disturbance severity (Hobbs and Huenneke 1992; Stohlgren et al. 1999b; Crawford et al. 2001; Keeley et al. 2002). In this study, only char depth, a proxy for fire severity was a consistent predictor for cover of exotic species in our models at least up to four years post-fire. Other abiotic variables such as nitrogen and elevation were significant one year after the fire but the effects were inconclusive three years later. Fire severity seemed to be the most important physical predictor of exotics species establishment after a wildfire at the 1-m^2 and the 1000-m^2 and scales and in both years.

Biotic factors seemed to be much more significant in determining where exotic plants establish. I consistently found positive relationships between exotic species cover and native species richness and negative relationships between exotic species cover and native grass cover, the dominant understory plant type in this system. While other studies have found conflicting results at different scales of measurement (Stohlgren et al. 1999b; Naeem et al. 2000), I found these biotic relationships to be consistent in both years and at both scales of measurement. This suggests that dominant species exert a greater control over invasibility of post-fire systems than sub-dominant species. Dominant species tend to produce more biomass restricting establishment of both native sub-species and exotic species (Robinson et al. 1995). However, not all studies have shown that dominant species exert greater control over invasibility at the neighborhood (1-m^2) scale (Smith et al 2004). In this study, I showed that cover of dominant species restricts establishment of exotic species at the neighborhood scale and this reflects where exotics establish at the larger scale (1,000-m^2).

Seeded grasses seem to have a very different impact on invasibility than native grasses that reestablish naturally after a fire. Since seeded grasses often result in high vegetative cover and can become a dominant species (Beyers 2004), one might expect them to also prevent establishment of exotic species. However, I found a positive relationship between exotic species cover and seeded grass cover at both scales and in both years. This is particularly telling since cover of seeded and native grasses was very similar in the first year after the fire regardless of fire severity (chapter 4). Also, Pearson correlation coefficients were rather low at the 1-m^2 scale between char depth and seeded grass cover in 2001 (0.24, $p < 0.0001$) and native grass cover in 2001 (-0.43, $p < 0.0001$). I suspect that this relationship is partly a result of the effects of char, but also exists because of contamination of seed mixes with other exotic species. At Cerro Grande, about 32.7 kg of seed were applied to approximately 7,000 ha. Only a small portion of this mix was tested in a seed purity analysis. That analysis found a small percentage (about 1%) of the seed mix was composed of weedy species that are common in disturbed lands and agricultural areas. While this percentage may be insignificant when applying small amounts of seed, it may become substantial when large amounts are applied to broad areas. Furthermore, such analysis typically includes only species that are included on a state's noxious weed list (USDA, Federal Seed Act, 2004). Thus, species that are not classified as noxious but still have significant ecological impacts (such as *Bromus tectorum*) may have large quantities in the seed mix. In this study *Bromus tectorum* was the most frequently encountered exotic species in the burned area in both years.

I conclude that fire severity is probably the best abiotic variable to predict where exotic plant species will establish after a wildfire. However, biotic variables seem to be better predictors for cover of exotic species. The cover of dominant native species may discourage establishment of exotic species after wildfires, more so than cover of other species. The cover of native grasses may be a function of numerous abiotic factors including fire severity. Seeding treatments may enhance exotic species establishment. Some evidence suggests that they may also inhibit native plant recovery (chapter 3). Given that post-fire seeding treatments have been shown to be ineffective in reducing soil erosion in some cases (Wagenbrenner 2003), and they may have unintended consequences such as introduction of exotic species and decreased recovery of native species, their cost and widespread use may be difficult to justify is some areas. Perhaps methods of rehabilitation that encourage recovery of dominant species would be most beneficial to short and long-term recovery of burned areas. If use of seed mixes after a wildfire seems justified in any particular case, more rigorous standards for testing of purity and follow up monitoring should be used to assure exotic species are not introduced.

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Table 1: Grass species used for post-fire rehabilitation treatments within the 2000 Cerro Grande burn, NM. The two native grasses in the mix were assumed to be insignificant in the study area prior to the wildfire.

Species	Classification	Grass type
Hordeum vulgare L.	Exotic	Annual
Lolium multiflorum Lam.	Exotic	Annual
Elymus trachycaulus (Link) Gould ex Shinners	Native	Perennial
Bromus carinatus Hook. & Arn.	Native	Perennial

Table 2: Tested models and corresponding predictors for data taken in 2001 within the Cerro Grande fire, Jemez Mountains, New Mexico. In each model exotic species cover at the 1000-m^2 scale is the dependent variable. All models are of the form $y = \beta_0 + x_1\beta_1 + .. x_n\beta_n$ where n is the number of parameters in the model. Seed01 = seeded grass percent cover in 2001, richness01 = native species richness in 2001, grass01 = native grass percent cover in 2001, nitrogen = total soil nitrogen (%), clay = soil clay content (%), char = mean char depth.

Model	Parameters
1	Radiation elevation clay
2	Char canopy nitrogen
3	Richness01 grass01 seed01
4	Char canopy nitrogen richness01 grass01 seed01
5	Radiation elevation clay richness01 grass01 seed01
6	Radiation elevation clay char canopy nitrogen
7	Radiation elevation clay char canopy nitrogen richness01 grass01 seed01

Table 3: Tested models and corresponding predictors for data collected in 2004 within the Cerro Grande fire, Jemez Mountains, New Mexico. In each model exotic species cover at the 1000-m^2 scale is the dependent variable. All models are of the form $y = \beta_0 + x_1\beta_1 + .. x_n\beta_n$ where n is the number of parameters in the model. Exotic01 = exotic species cover in 2001, richness04 = native species richness in 2004, seed04 = seeded grass cover in 2004, grass04 = native grass cover in 2004. See table 2 for other abbreviations.

Model	Predictors
1	Radiation elevation clay
2	Char canopy nitrogen
3	Richness01 seed01 grass01 exotic01
4	Richness04 seed04 grass04
5	Char canopy nitrogen richness01 seed01 grass01 exotic01
6	Char canopy nitrogen richness04 seed04 grass04
7	Radiation elevation clay richness01 seed01 grass01 exotic01
8	Radiation elevation clay richness04 seed04 grass04
9	Radiation elevation clay char canopy nitrogen
10	Radiation elevation clay char canopy nitrogen richness01 seed01 grass01 exotic01
11	Radiation elevation clay char canopy nitrogen richness04 seed04 grass04

Table 4: Models and corresponding predictors using data from 1- m^2 plots collected in 2001 within the Cerro Grande fire, Jemez Mountains, New Mexico. Exotic species cover in 2001 in 1-m^2 plots is the dependent variable All models are of the form $y = \beta_0 + x_1\beta_1 + .. x_n\beta_n$ where n is the number of parameters in the model. Veg = vegetation type, soil01 = cover of bare ground (%) in 2001. See table 2 for other abbreviations.

Model	Predictors
1	Veg aspect
2	Char soil01
3	Seed richness01 grass01
4	Veg aspect seed01 richness01 grass01
5	Char soil01 seed01 richness01 grass01
6	Veg aspect char soil01 seed01 richness01 grass01

Table 5: Models and corresponding predictors using data from 1-m^2 plots collected in 2004 within the Cerro Grande fire, Jemez Mountains, New Mexico. Exotic species cover in 2004 in 1-m^2 plots is dependent variable. All models are of the form $y = \beta_0 + x_1\beta_1 + .. x_n\beta_n$ where n is the number of parameters in the model. Soil04 = cover of bare ground in 2004. See tables 3 and 4 for other abbreviations.

Model	Predictor
1	Veg aspect
2	Char soil01
3	Char soil04
4	Seed01 grass01 rich01 exotic01
5	Seed04 grass04 rich04
6	Veg aspect seed01 grass01 rich01 exotic01
7	Veg aspect seed04 grass04 rich04
8	Char soil01 seed01 grass01 rich01 exotic01
9	Char soil04 seed04 grass04 rich04
10	Veg aspect char soil01 seed01 grass01 rich01 exotic01
11	Veg aspect char soil04 seed04 grass04 rich04

Table 6: ANOVA table for model with exotic species cover as dependent variable and year (2001 and 2004), vegetation type (mixed conifer, ponderosa pine, and pinyon-juniper), fire severity (high, low, and unburned) and their interaction as independent variables. N = 68.

Source	df	*F*	p
Model	15	3.50	0.0004
Error	52		
Year	1	4.89	0.0314
Vegetation type	2	4.21	0.020
Fire severity	2	6.07	0.0043
Year*vegetation type*fire severity	10	2.77	0.0081

Table 7: Models for data in treated plots at 1000 m^2 scale in 2001 and their associated AICc, delta AICc, and weights. See table 1 for a description predictor abbreviations. N = 34 for all models. Models 4, 6, and 7 were used for averaging parameter estimates.

Model	AICc	ΔAICc	Weight	Predictors
1	77.619	26.485	0.00001	Radiation elevation clay
2	65.069	13.935	0.001	Char canopy nitrogen
3	62.962	11.827	0.003	Richness01 grass01 seed01
4	52.303	1.169	0.313	Char canopy nitrogen richness01 grass01 seed01
5	67.535	16.401	0.0002	Radiation elevation clay richness01 grass01 seed01
6	54.181	3.047	0.123	Radiation elevation clay char canopy nitrogen
7	51.134	0	1.000	Radiation elevation clay char canopy nitrogen richness01 grass01 seed01

Table 8: Model averaged parameter estimates and associated standard error averaged from three models that showed significant support given the data. Data are for exotic species cover in 2001 at the 1000-m^2 scale. Estimate refers to the slope estimate of the given parameter in relation to cover of exotic species. SE refers to the standard error of the associated parameter estimate.

Parameter	Estimate	SE
Char	5.199	2.751
Canopy	-0.003	0.020
Nitrogen	-10.999	2.808
Richness01	0.157	0.055
Grass01	-0.747	0.566
Seed01	0.116	0.077
Radiation	1.760	1.892
Elevation	0.003	0.002
Clay	0.122	0.074

Table 9: Models for data in 2004 at the 1000 m^2 scale and their associated AICc, delta AICc, and weights. See table 3 for a description predictor abbreviations. N = 34 for all models. Models 1, 2, 3, 6, 7, 8, 9, 10, and 11 were all used for averaging parameter estimates.

Model	AICc	ΔAICc	Weight	Parameters
1	13.144	8.701	0.005	Radiation elevation clay
2	9.218	4.775	0.032	Char canopy nitrogen
3	12.925	8.482	0.005	Rich01 seed01 grass01 exotic01
4	14.527	10.084	0.002	Rich04 seed04 grass04
5	16.299	11.856	0.001	Char canopy nitrogen rich01 seed01 grass01 exotic01
6	8.179	3.737	0.054	Char canopy nitrogen rich04 seed04 grass04
7	5.798	1.355	0.177	Radiation elevation clay rich01 seed01 grass01 exotic01
8	4.443	0	0.349	Radiation elevation clay rich04 seed04 grass04
9	5.584	1.141	0.197	Radiation elevation clay char canopy nitrogen
10	12.246	7.803	0.007	Radiation elevation clay char canopy nitrogen rich01 seed01 grass01 exotic01
11	5.880	1.437	0.170	Radiation elevation clay char canopy nitrogen rich04 seed04 grass04

Table 10: Model averaged parameter estimates and associated standard error developed from nine models that showed significant support given the data. Data are for exotic species cover in 2004 at the 1000-m^2 scale. Estimate refers to slope estimate of the given parameter in relation to cover of exotic species. SE refers to the standard error associated with the parameter estimate.

Parameter	Estimate	SE
Radiation	1.880	1.283
Elevation	-0.003	0.001
Clay	0.035	0.039
Char	0.590	0.257
Nitrogen	-0.693	1.887
Canopy	0.001	0.011
Rich01	0.042	0.025
Grass01	-0.060	0.035
Seed01	0.042	0.038
Exotic01	0.104	0.078
Rich04	0.052	0.030
Grass04	-0.007	0.031
Seed04	0.076	0.036

Table 11: Models for data in treated plots at 1-m^2 scale in 2001 and their associated AICc, delta AICc, and weights. See table 1 for a description predictor abbreviations. N = 340. Models 3, 4, and 5 were used for averaging parameter estimates.

Model	AICc	ΔAICc	Weight	Predictors
1	-615.926	35.286	<0.0001	Veg aspect
2	-618.711	32.501	<0.0001	Char soil01
3	-651.212	0	0.845	Seed01 richness01 grass01
4	-643.712	7.500	0.020	Veg aspect seed01 richness01 grass01
5	-647.538	3.674	0.135	Char soil01 seed01 richness01 grass01
6	-629.170	22.042	<0.0001	Veg aspect char soil01 seed01 richness01 grass01

Table 12: Model averaged parameter estimates and associated standard error developed from three models that showed significant support given the data. Data are for exotic species cover in 2001 in 1-m^2 plots. Estimate refers to either the intercept or slope estimate for the parameter in relation to exotic species cover. SE refers to the standard error of the parameter estimate.

Estimate type	Parameter	Estimate	SE
Slope	Seed01	-0.0004	0.030
Slope	Richness01	0.145	0.026
Slope	Grass01	-0.151	0.030
Slope	Char	0.016	0.028
Slope	Soil01	-0.0003	0.008
Intercept	Ponderosa pine	0.062	0.056
Intercept	Mixed conifer	-0.016	0.062
Intercept	Pinyon-juniper	0.046	0.060
Intercept	North	0.062	0.056
Intercept	South	0.009	0.043

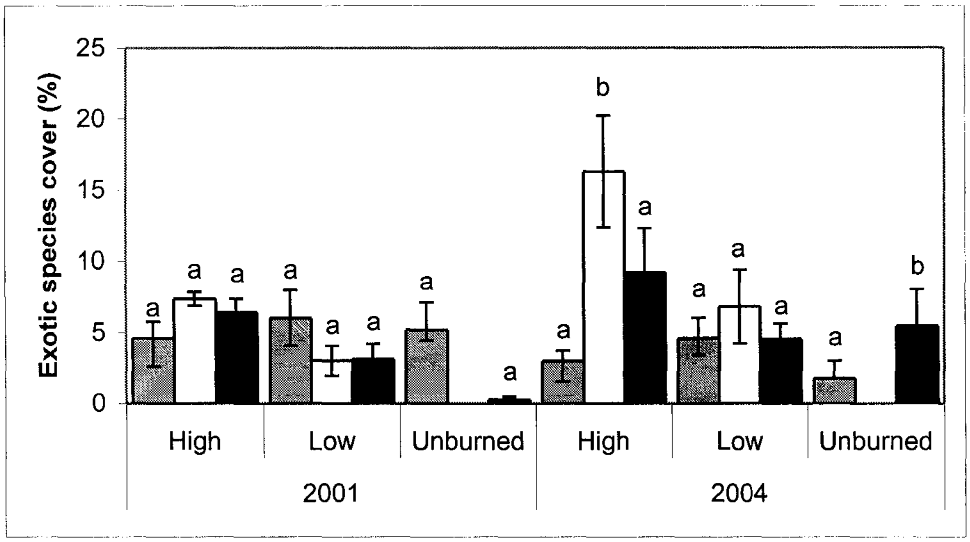
Table 13: Models for data in 2004 at the 1-m^2 scale and their associated AICc, delta AICc, and weights. See tables 1 and 2 for description predictor abbreviations. N = 340 for all models. Models 7, 10, and 11 were used for averaging parameter estimates.

Model	AICc	ΔAICc	Weight	Parameters
1	-387.807	30.616	<0.0001	Vegetation aspect
2	-384.179	34.242	<0.0001	Char soil01
3	-382.162	36.259	<0.0001	Char soil04
4	-365.094	53.327	<0.0001	Seed01 grass01 rich01 exotic01
5	-366.838	51.583	<0.0001	Seed04 grass04 rich04
6	-401.823	16.598	0.0002	Vegetation aspect seed01 grass01 rich01 exotic01
7	-415.877	2.544	0.164	Vegetation aspect seed04 grass04 rich04
8	-387.774	30.647	<0.0001	Char soil01 seed01 grass01 rich01 exotic01
9	-383.792	34.629	<0.0001	Char soil04 seed04 grass04 rich04
10	-416.744	1.677	0.252	Vegetation aspect char soil01 seed01 grass01 rich01 exotic01
11	-418.821	0	0.584	Vegetation aspect char soil04 seed04 grass04 rich04

Table 14: Model averaged parameter estimates and associated standard error developed from three models that showed significant support given the data. Data are for exotic species cover in 2004 at the 1-m^2 scale. Estimate refers to either the intercept or slope estimate for the parameter in relation to exotic species cover. SE refers to the standard error of the parameter estimate.

Estimate type	Parameter	Estimate	SE
Slope	Seed01	0.099	0.049
Slope	Seed04	0.146	0.047
Slope	Grass01	-0.131	0.058
Slope	Grass04	-0.067	0.039
Slope	Rich01	0.036	0.045
Slope	Rich04	0.046	0.046
Slope	Soil01	0.022	0.012
Slope	Soil04	-0.003	0.013
Slope	Exotic01	-0.055	0.076
Slope	Char	0.088	0.037
Intercept	North	0.502	0.073
Intercept	South	0.487	0.110
Intercept	Mixed conifer	-0.165	0.105
Intercept	Ponderosa pine	0.487	0.110
Intercept	Pinyon-juniper	0.151	0.081

Figure 1: Percent cover of exotic species in 2001 and 2004 in areas of different fire severity and vegetation types. Gray bars represent mixed conifer plots, white bars represent ponderosa pine plots, and black bars represent pinyon-juniper plots. Error bars represent standard error. N = 34. Different letters represent a significant difference between years within fire severity and vegetation type classes at the $p<0.05$ level.



CHAPTER 6: Conclusion

Burned areas rehabilitation treatments are applied for the benefit of reducing runoff and soil erosion. These potential benefits should be weighed against potential ecological costs associated with these treatments. However, knowledge on the potential costs and benefits, particularly of grass seeding treatments, has been lacking. The purpose of my dissertation research is to better understand the potential costs of one of the more commonly used rehabilitation treatments; post-fire grass seeding with exotic grasses or cultivars of native grasses. In particular I determined how grass seeding impacts recovery of native grasses, native species richness, and establishment of exotic species. I examined the potential impacts of seeded grasses in four integrated studies.

Specifically I examined the propagule pressure of native and seeded grasses and discovered that the density of seeds from seeded grasses is much higher than that of native grasses in areas of high and moderate fire severity and this corresponded to a high density of seeded grasses and low density of native grasses in the above ground vegetation. Even though native grass seed was present in the seed bank in all categories of fire severity, they were not well represented in the above ground vegetation in areas where seeded grasses dominated the seed bank. This was likely a function of both the low density of native grass seeds and the high density of seeded grass seeds.

I addressed the potential for high cover of seeded grasses in areas of high fire severity to deter establishment of native grasses and found that native grass seedling recruitment decreased with increasing cover of seeded grasses and increasing cover of straw mulch. Seeded grasses responded very differently than native grasses to environmental variables. Seeded grass seedling recruitment did not decrease with increasing cover of seeded grasses, but increased with increasing density of seeded grass seeds in the seed bank.

I also found that the potential for exclusion of native grasses by seeded grasses may also be a function of their response to availability of resources such as light and nitrogen. Seeded grasses exhibit higher growth rates than native grasses when nitrogen availability was high. This effect seemed to be important on a landscape scale as cover of seeded grasses increased up to four years after the fire in areas with high nitrogen availability (mixed conifer forests) and decreased in areas of low nitrogen availability (pinyon-juniper forests). In areas were seeded grasses increased in cover four years after the fire there was lower cover of native grasses which may be an indication that seeded grasses are deterring native grass establishment in those areas. However, native grasses increased in cover in all vegetation types despite the persistence of seeded grasses. Overall, native and seeded grasses seemed to have very different effects on native species richness. Native species richness was consistently positively correlated with native grass cover and negatively correlated with seeded grass cover.

The impacts of post-fire seeding treatments on establishment of exotic species have not previously been addressed on a large scale, so I provided evidence that grass seeding treatments encouraged rather than deterred establishment of exotic species. This was probably compounded by the effect disturbance severity (char depth). I again showed that native grasses had a very different effect than seeded grasses. Exotic species cover was consistently negatively correlated with native grass cover and positively correlated with seeded grass cover. These factors seemed to be much more important in predicting exotic species cover than other factors (e.g., nitrogen, elevation, clay content).

The research conducted in this dissertation is a significant contribution to the fields of science and land management. I provide quantitative evidence to confirm theories in invasion biology that suggested that propagule pressure and growth response to available resources were important factors in determining a species' ability to dominate a vegetation community. I confirmed that exotic species were generally positively associated native species richness and negatively associated with increased cover of dominant species, a subject that has been hotly debated in recent scientific literature. Also, I showed that these relationships were consistent at both small and large spatial scales. I provide descriptive information of seed banks and vegetation in post-fire communities, data that have not been widely available to natural area managers or policy makers. Finally, I provide evidenced for the potential negative ecological effects of post-fire seeding, including suppressed native species richness, determent of native grass establishment, and the introduction and spread of exotic species. This information will be particularly useful to managers when planning post-fire rehabilitation treatments or monitoring the effects of fire and other fire management practices.