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Seed supply of native and cultivated grasses in pine forests of the southwestern United States and the potential for vegetation recovery following wildfire

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Abstract

In this study we examined seed supply (seed banks and seed rain) and vegetation of seeded cultivated grasses and naturally occurring native grasses following a wildfire in northern New Mexico, USA. We specifically examined density of native and cultivated grass seeds and plants in areas of high, moderate, and low fire severity. We also examined the similarity between density of native and cultivated grass seeds to density of above ground plants. Density of native grass seed per square meter was higher in areas that burned under low fire severity (85.18 ± 44.83) compared to areas of moderate (18.52 ± 11.26) and high (7.41 ± 4.90) fire severity; however, differences were not statistically significant due, in part, to the high error associated with estimates. Density of cultivated grass seed per square meter was higher than that of native grass seed in areas of high (439.60 ± 117.98) and moderate (437.02 ± 146.50) fire severity, areas that were seeded with cultivated grasses after the wildfire for erosion control. Density of seeded grass plants per square meter was also higher than that of native grass plants in areas of high (18.78 ± 4.59 versus 0.33 ± 0.24) and moderate (8.22 ± 1.76 versus 0.22 ± 0.15) fire severity. There was a higher correspondence between the density of cultivated grass seeds and plants (highest value 0.32 ± 0.11) compared to density of native grass seeds and plants (highest value 0.05 ± 0.04). The high density of seeds, plants, and correspondence indicated that seeds from cultivated grasses are more likely to establish as post-fire vegetation than seeds from native grasses. Seeding with cultivated grasses following a wildfire may slow or inhibit recovery of native grasses in the short term. Longer-term implications for site occupancy deserve further study.

Introduction

Seed banks and seed rain (seed supply) can be important sources of recovering vegetation following a disturbance (Parker et al. 1989). Alteration in disturbance regimes can change the density and composition of the seed supply, and thus lead to a subsequent change in the above ground vegetation following a disturbance (Archibold 1989). In ponderosa pine systems (*Pinus ponderosa* P. & C. Lawson) in the southwestern United States, a century of overgrazing and fire suppression have contributed to increased tree and shrub canopy cover and increased loading of surface fuels (i.e. litter, woody debris), decreased availability of light and soil resources, and decreased availability of suitable microsites for seed germination (due to increased litter loading) (Covington and Moore 1994). This has led to decreases in understory species cover, particularly for perennial grasses (Cooper 1960; Covington and Moore 1994). Grass seed banks are typically short-lived and rely on continued seed rain from nearby plants (Rice 1989). A reduction in cover of native grasses should result in reduced seed rain, reduced inputs to the seed bank, and thus, maintenance of low grass cover. While there have been no studies that specifically examine the impacts of changing disturbance regimes on grass seed supply in southwestern ponderosa pine forests, it is reasonable to expect that the density of native grass seed supply has been reduced along with the documented decrease in cover of native grasses. Wildfire, particularly of high severity, may further deplete the seed supply. While native grasses in this system are well adapted to fire of low intensity, often exhibiting increased seed and flower production (Ehrenreich and Aikman 1963), they are not well adapted to fires of uncharacteristic high intensity, and often experience increased fire-induced seed and plant mortality which can lead to a delay in post-fire native grass recovery (Armour et al. 1984; Korb et al. 2004). Long distances from available seed sources outside the fire perimeter may further delay the recovery of native grasses after large wildfires.

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. Exotic grasses or native cultivars (seeded grasses) are often used because of their wide availability, low cost, and ability to germinate and establish rapidly under a variety of conditions (Robichaud et al. 2000). The same factors that allow these species to establish and grow rapidly, may also make them superior competitors over native grasses. 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 in arid systems (Melgoza et al. 1990; Brooks 2003). Increased propagule pressure is another important factor that may influence successful dominance of an exotic species, with high seed rain of an exotic species increasing the likelihood of dominance by that species (Levine 2001). Low supply of native grass seed following large wildfires of high intensity, coupled with the application of large amounts of exotic grass seed could cause the seeded grasses to dominate the propagule supply, and thus the above ground vegetation. Further, if seeded grasses are also superior competitors over native species they could dominate post-fire systems for some time, ultimately preventing native plant recovery and reducing native plant diversity (Griffin 1982; Conard et al. 1995; O'Leary 1995).

Many seed bank studies have reported lack of correspondence between the seed bank and the vegetation (Major and Pyott 1966). Different species often have differing levels of correspondence between their seed banks and vegetation, partly because different species respond to their environment in varying ways (Rice 1989). High correspondence between the seed bank and the vegetation can be a good indication of a species' ability to germinate and establish. 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). Other species need specific environmental conditions to germinate, or produce few seeds, and thus are more likely to have a low correspondence between the seed bank and the vegetation (Pierce and Cowling 1991; Chambers 1993). We may expect seeded grasses to have a high correspondence between the seed bank and vegetation because they are cultivars that are often bred for rapid germination and establishment. However, high seed density can also be detrimental to establishment of certain species, decreasing the correspondence between the seed bank and vegetation (McMurray et al. 1997). A higher correspondence value for seeded grasses compared to native grasses may be an indication of seeded grasses' stronger establishment and competitive ability.

In this study, we examined the dynamics of the seed supply (seed bank and seed rain) and above ground vegetation for seeded grasses and native grasses in a burned ponderosa pine forest in northern New Mexico, USA. We also addressed how seed supply and plant abundance vary between native and seeded grasses in areas of different fire severity, and areas that were or were not seeded with grasses for post-fire erosion control. We examined how both factors may impact long-term recovery of native grasses in southwestern ponderosa pine forests after erosion control treatments (seeding) following wildfires. Specifically we addressed the following questions:

Does the dominance of native or seeded grasses in the seed bank and the above ground vegetation vary in areas of different fire severity and areas that were seeded with exotic or cultivated grasses for erosion control?

How does seed density of native and seeded grasses correlate with density of above ground vegetation in areas of different fire severity and areas that were seeded with exotic or cultivated grasses for erosion control?

We expected density of seeded grasses to be highest in areas where post-fire seeding treatments were implemented (high and moderate fire severity) and density of native grass seed to be highest where fire-induced seed mortality would have been low (low fire severity). We also expected seeded grasses to have higher competitive ability than native grasses, and thus a higher correspondence between the seed bank and vegetation.

Study site

This study was conducted at the Cerro Grande burn which burned 17,352 ha in May of 2000 in the vicinity of the town of Los Alamos in northern New Mexico, USA (35°52′ N, 106°19′ W). The fire burned primarily through ponderosa pine 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. However, the two native grasses used, while native to the state of New Mexico, are not common grass species in ponderosa pine forests in the southwest and were assumed to be insignificant in our study area prior to the wildfire (Foxx 1994). Thus, we 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. We 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). We examined these grasses along with four of the most common native perennial grasses in this system (Table 1). Nomenclature follows the NRCS Plants database (USDA, NRCS 2004). Seeds from the focal grasses in our study are likely to be persistent in the seed bank for less than 10 years (Fulbright et al. 1982; Springer 1999). Seeded grass seeds are likely to be viable for less than 5 years (Fulbright et al. 1982).

Table 1. Grass species examined in seed bank study within the 2000 Cerro Grande burn, NM.

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

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.

Within the Cerro Grande burned area, we focused our study in Rendija Canyon which is located adjacent to the town of Los Alamos in the Sante Fe National Forest, New Mexico (2280 m in elevation). Different areas in this canyon experienced low, moderate, and high fire severity all within close proximity to each other. We did not sample unburned areas as other seed bank studies in ponderosa pine have found similar or slightly lower estimates of seed density in lightly burned areas compared to unburned areas (Vose and White 1987; Springer 1999). Other variables that may influence the vegetation and seed bank (i.e., distance to roads, elevation, soil type) exhibited minimal variation within the study area. Areas classified as high and moderate fire severity within the study area were aerially seeded for erosion control at an average rate of (about 600 seeds/m^2) within two months of the fire. Seeds from the four seeded grass species had equal proportions in the seed mix. All seeded grass species were observed to establish and produce viable seed in the season they were applied. 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 randomly chosen in each fire severity class (high, moderate, and low). Fire severity was assessed using post-fire Landsat imagery and visually verified in the field through observations of scorch and consumption of tree crown needles based on a rating developed by Omi and Kalabokidis (1991). In each site one 50-m transect was placed parallel to the line of contour. Three 1-m^2 plots were randomly established along each transect. Since seed bank density has been shown to be spatially heterogeneous, often with higher density near parent plants (Major and Pyott 1966), we focused sampling efforts in areas with some grass cover (greater than 5%). Areas of transects dissected by patches of exposed bare soil (less than 5% vegetative cover) or other features (i.e. rock, shrubs) were excluded from study. Density of all grass species were sampled in each plot. Three soil samples were collected per plot with each sample encompassing a circular area with a 10 cm diameter to a depth of 5 cm. Seed bank samples and assessments of plant density were taken in the fall of 2001 (one year post-fire). Subsequent vegetation sampling was conducted in the spring and summer of 2002 (two years post-fire). Only newly established plants counted in the spring and summer samplings were included in plant density estimates. We assumed these plants established from the seed bank or seed rain collected in the fall of 2001. Individual plants were marked so that they would not be counted again in subsequent samplings. The species of interest in this study typically drop their seeds in the late summer and early fall and initiate growth in the spring or early summer (Vose and White 1987). Seeds from the focal grasses in this study remain viable for 3–8 years (Fulbright et al. 1983). However, seedling recruitment of grasses in this system is more a function of the number of seeds supplied in the seed rain (Vose and White 1987). We assumed that the seeds collected in our soil samples (including litter layer) would be from the persistent seed bank (seeds that were deposited greater than one year prior to collection) and the transient seed bank (seeds that were mostly from the seed rain deposited in the season prior to collection). For native grasses, both seed sources should be important for vegetation recovery. We conducted two vegetation samplings in the growing season (spring and summer) to capture more individuals in plant density estimates.

Soil samples collected from plots were placed in a refrigerator (5 °C) for two weeks for cold stratification. The focal species in this study have been found to readily germinate either with no cold treatment, or with a cold treatment ranging from 4 to 10 °C for 1–3 weeks (Fulbright et al. 1983). The soil samples were then laid out in thin layers in flats (36 × 36 cm) with potting soil (depth 7 cm) and placed in a heated greenhouse. In addition to natural light, plots received 4 h of artificial light per day and were misted with water every 4 h so that they remained moist. Seedlings emerging from flats were identified and recorded for 24 weeks. This is a preferred method for estimating seed density and diversity in seed banks (Gross 1990). Identified seedlings were immediately removed from flats. Seedlings that were not easily identified were transplanted into pots and allowed to grow until identifiable. Since a large number of samples are needed to assess the seed bank and vegetation of uncommon species (Benoit et al. 1989), we focused our seed density estimates on dominant species in this system which included native and seeded grasses (Table 1).

We estimated the density of seeds per square meter by multiplying the number of seedlings that emerged in the three soil samples (10 cm diameter) in each plot by 33.3. Using mixed model ANOVA we tested the effect of fire severity (high, moderate, and low), grass type (native and seeded) and their interaction on estimates of seed density. Plot number nested in fire severity class was treated as a random effect in the model. We also used a mixed model ANOVA to test the effects of fire severity, grass type and their interaction on density of individual grass plants in 1-m^2 plots. Plot nested in fire severity class was treated as a random effect in the mixed model.

Relative seed density and relative plant density were 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). We calculated relative density for each seed bank sample and vegetation plot. 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 for each grass type (Greig-Smith 1964);

$$\mathrm{SI} = \frac{2w}{a+b},$$

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 were recorded in both the seed bank sample and the vegetation plot. Similar methods were used by Ungar and Woodell (1996). 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 seeded grasses were more likely to establish than native grasses (have a higher SI), we compared the SI of seed density and plant density for both native and seeded grasses. A mixed model ANOVA was conducted to determine if SI depended on the grass type, fire severity, and their interaction. Plot replicate nested within fire severity class was treated as a random effect in the model. Plots with no seeds recorded in the seed bank are not included in w and are reported as missing values in the ANOVA model. All statistical analysis was conducted using the mixed model procedure (proc mixed) in the SAS statistical program (SAS Institute 1999).

Results

All species that emerged in the seed bank samples are recorded in Appendix 1. We focused statistical analysis on eight focal species (Table 1). When examining the mean density of seeds per square meter, we found the full model ($F = 2.00$, $\mathrm{df_{error}} = 24$, $n = 54$, $p = 0.044$) and the interaction between grass type and fire severity ($F = 6.54$, $p = 0.005$) to be significant. The mean density of native grass seed seemed to be higher in areas classified as low fire severity, although there was high variability associated with estimates and no significant difference in mean density of seeds of native grasses between areas of high, moderate and low fire severity (Table 2). Density of seeded grass seed was up to 60 times higher than density of native grass seed in areas where post-fire seeding took place (high and moderate fire severity) (Table 2). Density of seeded grass seed in these areas was also much higher than density of native grass seed in areas of low fire severity. There were very few seeds from seeded grasses in areas of low fire severity, where seeded grasses were not intentionally applied.

The mean density of plants per square meter showed similar trends to seed density. The full model ($F = 3.00$, $\mathrm{df_{error}} = 24$, $n = 54$, $p = 0.004$) was significant, as was the interaction between grass type and fire severity ($F = 18.20$, $p < 0.0001$). 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 3). Density of seeded grass plants was an order of magnitude higher than density of native grass plants in areas of high and moderate

Table 2. Mean number of seeds per square meter (and standard error) from native and seeded grasses in areas of low, moderate and high fire severity.

Fire severity	Native grass seed density	Seeded grass seed density
High	7.41 (4.90) a	439.60 (117.98) b
Moderate	18.52 (11.26) a	437.02 (146.50) b
Low	85.18 (44.83) a	14.82 (8.07) a

N = 54. Different letters represent significant differences at the $p < 0.05$ level. Low severity areas were not aerially seeded.

Table 3. Mean number of native and seeded grasses (and standard error) per square meter in areas of low, moderate, and high fire severity.

Fire severity	Native grass density	Seeded grass density
High	0.33 (0.24) a	18.78 (4.59) c
Moderate	0.22 (0.15) a	8.22 (1.76) b
Low	7.11 (1.92) b	0.33 (0.17) a

N = 54. Different letters represent significant differences at the $p < 0.05$ level. High and moderate severity areas received seeding treatment; low severity areas were not seeded.

Table 4. 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.

Fire severity	Native grass SI	Seeded grass SI
High	0 (0) a	0.27 (0.07) bc
Moderate	0 (0) a	0.32 (0.011) b
Low	0.05 (0.04) a	0 (0) ac

N = 41. Different letters represent significant differences at the $p < 0.05$ level.

fire severity (Table 3). There were very few seeded grasses in areas of low fire severity.

The full model testing the effects of grass type, fire severity, and their interaction on mean SI was significant ($F = 2.65$, $\mathrm{df}_{\mathrm{error}} = 11$, $n = 41$, $p = 0.045$). The sample size for SI was lower, as SI was not calculated for plots where no seeds were recorded in the seed bank. The effect of fire severity on SI was significant ($F = 7.44$, $p = 0.020$) and the interaction between fire severity and grass type was nearly significant ($F = 3.31$, $p = 0.075$). Mean SI was higher for seeded grasses versus native grasses in areas of high and moderate fire severity (Table 4). 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. 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 4).

Discussion

Our estimates of native grass seed and plant density in areas of low fire severity were similar to estimates in other burned and unburned ponderosa pine forests in the southwest (Vose and White 1987; Springer 1999). Previous studies have shown that low intensity fire can stimulate native grass seed and flower production (Ehrenreich and Aikman 1963), but such an increase in reproduction may have been hampered by a regional drought that occurred in the study area in 2001 and 2002. We are not aware of other studies that have examined seed supply of native and seeded grasses in more severely burned ponderosa pine forests. Native grass seed was present in all study sites, regardless of fire severity, indicating that seed supply of native grasses has not been completely depleted from the severely burned area. The presence of viable native seed indicates at least the potential for native grasses to reestablish the burned area from seed sources within the fire perimeter. If recovery was restricted by seed recruitment from further away, 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 was lower in areas that burned under high and moderate fire severity, indicating that seed mortality was higher in such areas or remnant living grasses were scarce. Density of seeded grass seed was much higher than that of native grasses in areas of high and moderate fire severity, presumably because of the seeding efforts in those areas. The fact that seeded grass seed was much higher than the highest density estimate of native grass seeds (low fire severity areas) suggests that seeded grasses are dominating the propagule pressure in the burned environment, which could lead to their dominance over native grasses (Levine 2001). This was supported by the fact that seeded grasses also had much higher plant density compared to native grasses in areas of high and moderate fire severity.

Seeded grasses may also have higher competitive ability than native grasses. The high SI 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. Cultivated grass varieties generally have less stringent requirements for germination than native grass species in semi-arid regions (Humphrey and Schupp 2002) and they are often bred to establish rapidly, have higher seed production, or be resistant to disease (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 (Hunter 2004), indicating a higher competitive ability. A strong competitive ability coupled with high propagule supply could allow seeded grasses to dominate and persist in such areas and possibly 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). We might 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 supply, 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 supply and vegetation up to 2 years after the treatments suggests that they will persist. In a related study we found that seeded grass cover increased in certain areas up to 4 years post-fire and this may have negative consequences for native species diversity (Hunter 2004). In other systems, persistence and dominance of seeded grasses have 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). It is yet unclear whether or not seeded grasses will persist in the long term. Persistence of seeded grasses varies widely and depends on a number of factors (Robichaud et al. 2000). However, post-fire treatments are implemented with the assumption that they will be beneficial or have benign impacts on native species recovery and diversity. Long-term monitoring of seeding treatments should be conducted to assure their effects on native grass recovery and native species diversity are not harmful.

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Appendix 1

Number of seedlings of all species recorded in all soil samples collected in areas of low, moderate and high fire severity.

Species	High severity	Moderate severity	Low severity
Amaranthus sp.	0	0	3
Arabis fendleri	0	0	1
Arabis sp.	0	0	4
Bahia dissecta	0	1	0
Bouteloua gracilis	7	2	0
Brassica sp.	0	2	0
Bromus carinatus	32	37	0
Carex sp.	0	0	5
Conyza canadensis	9	9	5
Elymus trachycaulus	3	1	0
Erigeron flagelaris	0	0	6
Erigeron speciosus	0	0	1
Hordeum vulgare	1	1	0
Lolium multiflorum	64	57	4
Koeleria macrantha	1	1	6
Monarda fistulosa	0	0	1
Poa fendleriana	0	9	0
Poa pratensis	0	1	0
Schizachyrium scoparium	2	0	18
Taraxacum officinale	3	0	0
Unknown forb	5	19	3
Unknown grass	0	2	2
Verbascum thapsus	1	0	43

References

Archibold O.W. 1989. Seed banks and vegetation processes in coniferous forests. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), Ecology of Soil Seed Banks, Academic Press Inc, San Diego, CA.

Armour C.D., Bunting S.C. and Neuenschwander L.F. 1984. Fire intensity effects on the understory in ponderosa pine forests. J. Range Manage. 37: 44–49.

Benoit D.L., Kenkel N.C. and Cavers P.B. 1989. Factors influencing the precision of soil seed bank estimates. Can. J. Bot. 67: 2833–2840.

Bock C.E., Bock J.H., Jepson K. and Ortega J.C. 1986. Ecological effects of planting African lovegrasses in Arizona. Natl. Geogr. Res. 2: 456–463.

Brooks M.L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. J. Appl. Ecol. 40: 344–353.

Cavers P.B. and Benoit D.L. 1989. Seed banks of arable land. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), Ecology of Soil Seed Banks, Academic Press, Inc, San Diego, CA.

Chambers J.C. 1993. Seed and vegetation dynamics in an alpine herb field – effects of disturbance type. Can. J. Bot. 71: 471–485.

Conard S.G., Beyers J.L. and Wohlgenmuth P.M. 1995. Impacts of post-fire grass seeding on chaparral systems – what do we know and where to we go from here? In: Scott T. (ed), Brushfires in California Wildlands: Ecology and Resource Management, International Association of Wildland Fire, Fairfield, WA.

Cooper C.F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecol. Monogr. 30: 130–164.

Covington W.W. and Moore M.M. 1994. Southwestern ponderosa forest structure – changes since Euro-American settlement. J. Forest. 92: 39–47.

DeBano L.F., Neary D.G. and Folliott P.F.1988. Fire's Effects on Ecosystems. New York, NY, John Wiley & Sons.

Ehrenreich J.H. and Aikman J.M. 1963. An ecological study of the effect of certain management practices on native prairie in Iowa. Ecol. Monogr. 33: 113–130.

Elliot K.J. and White A.S. 1987. Competitive effects of various grasses and forbs on ponderosa pine seedlings. Forest Sci. 33: 356–366.

Ferrandis P., Herranz J.M. and Martinez-Sanchez J.J. 2001. Response to fire of a predominantly transient seed bank in a Mediterranean weedy pasture (eastern-central Spain). Ecoscience 8: 211–219.

Foxx T.S. 1994. Vegetation succession after the La Mesa fire at Bandelier National Monument. In: Allen C.D. (ed.), Fire Effects in Southwestern Forests: Proceedings of the 2nd La Mesa Fire Symposium Los Alamos, New Mexico March 29–31, 1994. Gen. Tech. Rep. RM-GTR-286. Fort Collins, CO. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest Range and Experiment Station.

Fulbright T.E., Redente E.F. and Hargis N.E. 1982. Growing Colorado plants from seed: a state of the art. Vol. II: Grasses and Grasslike Plants. U.S. Dept. of Interior. Fish and Wildlife Service. FWS/OBS-82/29.

Greig-Smith P.1964. Quantitative Plant Ecology. Butterworths, Washington.

Griffin J.R. 1982. Pine seedling, native ground cover, and *Lolium multiflorum* on the marble-cone burn, Santa Lucia range, California. Madrono 29: 177–188.

Gross K.L. 1990. A comparison of methods for estimating seed numbers in soil. J. Ecol. 78: 1079–1093.

Gustafson D.J., Gibson D.J. and Nickrent D.L. 2004. Competitive relationships of *Andropogon gerardii* (Big Bluestem) from remnant and restored native populations and select cultivated varieties. Funct. Ecol. 18: 451–457.

Hassan M.A. and West N.E. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. Ecology 67: 269–272.

Humphrey D.L. and Schupp E.W. 2002. Seedling survival from locally and commercially obtained seeds on two semiarid sites. Restor. Ecol. 10: 88–95.

Hunter M.E. 2004. Post-fire grass seeding for rehabilitation and erosion control: implications for native plant recovery and exotic species establishment. Ph.D. Dissertation, Colorado State University.

Interagency Burned Area Emergency Stabilization and Rehabilitation (ESR) Handbook, version 2. http://fire.fws.gov/ifcc/Ers/handbook/.

Korb J., Johnson N. and Covington W. 2004. Slash pile burning effects on soil biotic and chemical properties and plant establishment: recommendations for amelioration. Restor. Ecol. 12: 52–62.

Levine J.M. 2001. Local interactions, dispersal, and native and exotic plant diversity along a California stream. Oikos 95: 397–408.

Major J. and Pyott W.T. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of flora. Vegetatio 13: 253–282.

McMurray M.H., Jenkins S.H. and Longland W.S. 1997. Effects of seed density on germination and establishment of a native and an introduced grass species dispersed by granivorous rodents. Am. Midland Nat. 138: 322–330.

Melgoza G., Nowak R.S. and Tausch R.J. 1990. Soil-water exploitation after fire – competition between *Bromus tectorum* (cheatgrass) and two native species. Oecologia 83: 7–13.

O'Leary J.F. 1995. Potential impacts of emergency seeding on cover and diversity patterns of Californian shrubland communities. In: Scott T. (ed), Brushfires in California Wildlands: Ecology and Resource Management, International Association of Wildland Fire, Fairfield, WA.

Omi P.N. and Kalabokidis K.D. 1991. Fire damage on extensively vs. intensively managed forests stands in the north fork fire, 1988. Northwest Sci. 65: 149–157.

Parker V.T., Simpson R.L. and Leck M.A. 1989. Pattern and process in the dynamics of seed banks. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), Ecology of Soil Seed Banks, Academic Press ,Inc, San Diego, CA.

Pierce S.M. and Cowling R.M. 1991. Disturbance regimes as determinants of seed banks in coastal dune vegetation of the southeastern cape. J. Veget. Sci. 2: 403–412.

Rice K.J. 1989. Impacts of seed banks on grassland community structure and population dynamics. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), Ecology of Soil Seed Banks, Academic Press, Inc, San Diego, CA.

Robichaud P.R., Beyers J.L. and Neary D.G. 2000. Evaluating the effectiveness of post-fire rehabilitation treatments. Gen. Tech. Rep. RMRS-GTR-63. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, US.

SAS1999. SAS/STAT Users' Guide. SAS Institute Inc., Cary, NC.

Springer J.D. 1999. Soil seed bank in southwestern ponderosa pine: implications for ecological restoration. M.S. Thesis, Northern Arizona University.

Ungar I.A. and Woodell S.R.J. 1996. Similarity of seed banks to aboveground vegetation in grazed and ungrazed salt marsh communities on the Gower peninsula, South Wales. Int. J. Plant Sci. 157: 746–749.

U.S. Department of Agriculture, Natural Resource Conservation Service. 2004. The PLANTS Database, version 3.5 (http://plants.usda.gov) National Plant Center, Baton Rouge, LA, USA.

van der Valk A.G. and Pederson R.L. 1989. Seed banks and the management and restoration of natural vegetation. In: Leck M.A, Parker V.T. and Simpson R.L. (eds), Ecology of Soil Seed Banks, Academic Press, Inc, San Diego, CA.

Vose J.M. and White A.S. 1987. Processes of understory seedling recruitment 1 year after prescribed fire in an Arizona ponderosa pine community. Can. J. Bot. 65: 2280–2290.