

EFFECTS OF FIRE AND POST-FIRE SEEDING ON PLANT COMMUNITIES IN A
PONDEROSA PINE FOREST

Melissa A. McMaster

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Approved:

Andrea Thode, Ph.D., Co-chair

Michael Kearsley, Ph.D., Co-chair

Peter Z. Fulé, Ph.D.

Margaret M. Moore, Ph.D.

ABSTRACT

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MELISSA A. MCMASTER

Changing climatic conditions coupled with altered forest conditions and fire regimes have resulted in fires outside the historical range of variability. While fire is an essential disturbance in ponderosa pine (*Pinus ponderosa* var. *scopulorum* Lawson) ecosystems, high severity crown fires as opposed to the historical low severity surface fires, create a vulnerable landscape. The immediate loss of vegetative cover after a fire leads to concerns of soil erosion and invasion by exotic plants and often drives post-fire rehabilitation. I tested the effects and effectiveness of seeding and the overall response of vegetation to varying fire severities in the Warm Fire. In my study, seeding with *Lolium perenne* ssp. *multiflorum* (L.) did not provide adequate vegetative cover to decrease soil erosion and was no more effective at preventing exotic invasions than natural recovery. My results suggest that presence of the seeded species may have led to a decrease of annual and biennial forbs and three native bunchgrasses. The community composition was significantly different between seeded and non-seeded plots in all three years and is changing at a similar rate but possibly in different trajectories. This study adds to the growing body of evidence that post-fire seeding falls short of management goals and may have unintended consequences on the native plant community.

In addition to the effects of seeding on post-fire plant communities, I compared the effects on vegetation of both low and high severity fire compared to unburned

controls. Native vegetation in the ponderosa pine ecosystems is adapted to the historic fire regime of frequent low severity surface fires. I found areas that had burned in low severity fire responded with increased species richness but no increase in total vegetative cover and were compositionally more similar to unburned controls. In my study, high severity fire was strongly correlated with increased species richness, increased annual and biennial forbs, and increased vegetative cover. While disturbances that occur at intermediate frequency and severity often produce the greatest diversity, in this case the accumulation of litter and duff may have precluded plant establishment in areas that burned at low severity. This study supports the continuation of reintroducing fire to ponderosa pine forests in northern Arizona as a means to improve forest health and sustainability by altering understory plant communities.

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PREFACE

This thesis contains two chapters intended for publication and is written in manuscript format. The manuscripts are Chapter 2: “Effects of post-fire seeding on plant communities in a high-severity wildfire” and Chapter 3: “Plant response to low and high severity fire in a ponderosa pine forest”. Tables, figures, and a list of literature cited appear at the end of each chapter. Chapters 2 and 3 use “we” instead of “I” because these papers have co-authors.

Chapter One

Literature Review

Wildfires are a natural and significant disturbance in ecosystems across the U.S. but alterations to the landscape from humans and changing climatic conditions have reduced the role of fire in shaping these systems (Agee 1998; Westerling et al. 2006). Fire is integral to maintaining the stability and sustainability of forest health in facilitating the architecture of overstory trees, composition of vegetation communities and nutrient cycling (Cooper 1960; Fulé et al. 1997). Ponderosa pine (*Pinus ponderosa* var. *scopulorum* C. Laws.) ecosystems in the Southwest are strongly influenced by fire and have been particularly impacted by over a century of fire suppression, grazing and timber extraction (Cooper 1960; Agee 1998). Early descriptions of ponderosa pine forests depict open parks with clusters of large diameter old growth pine trees interspersed with various mixed aged pine trees (Lang and Stewart 1910; Cooper 1960); this is quite contrary to the forests of the American Southwest today that have little understory vegetation and numerous small diameter trees. Current forest conditions are vastly different in structure, function and ecological processes (Covington and Moore 1994; Allen et al. 2002). The interactions of historic land use and climate change have resulted in high levels of fuel loading which have produced historically uncommon frequent, large and severe stand replacing crown fires (Covington and Moore 1994; Allen et al. 2002). The effects of these fires include increased post-fire tree mortality (McHugh and Kolb 2003), initial decreases of understory plant cover (Springer et al. 2004; Hunter et al. 2006) and the subsequent susceptibility of the landscape to invasion of non-natives, soil erosion and flooding (Beyers 2004; Keeley 2004; Hunter et al. 2006).

The historical fire regimes in the semi-arid ponderosa pine forests consisted of frequent, medium sized, low intensity, low severity, grass-fueled fires every 2-20 years which created a spatially heterogeneous landscape (Swetnam and Baisan 1996; Fulé et al. 1997; Allen et al. 2002). Fires were most common in June and July during the dry months preceding monsoon season and were ignited by lightning. Fire suppression and grazing over the last century has led to increase in fire severity and decrease in forest openings and spatial variability (Agee 1998). The recent increase of crown fires in southwest ponderosa pine forests is of major concern as there is the potential to change the trajectory of forest structure outside the historical range of natural variability (Savage and Mast 2005). Savage and Mast (2005) predict that forest regeneration will follow one of three potential trajectories: either there will be a flush of ponderosa pine seedlings leading to another dense and unsustainable forest structure; conifer regeneration will not occur and the vegetation community will shift to one of shrubs and/or grasses; or the forest will recover to an open ponderosa pine forest with clumped patches of ponderosa pine. Ponderosa pine trees are a “foundation species” in northern Arizona forests that define the forest architecture and functional ecology and a major shift in the trajectory of forest structure due to crown fires may continue to alter the forest ecosystem structure and function (Ellison et al. 2005).

Historical land use including grazing and logging, and climatic variation are intertwined factors that determine the number, severity, and frequency of fires in a given area. While historical land use is undeniably important in ponderosa pine forests, drought, variable moisture and higher temperatures associated with climate change play a significant role as well (Allen et al. 2002; Westerling et al. 2006). Specifically, there is a

strong correlation between unusually warm/dry winters, summer drought and increased fires with area burned in southwest ponderosa pine forests (McKenzie et al. 2004; Westerling et al. 2006). We see these effects with the Cerro Grande Fire in New Mexico in 2000, the Rodeo-Chediski Fire in 2002 and the Warm Fire in 2006. These three fires burned in part as high severity crown fires, outside the historical fire regime (GAO 2000; USAD/USNF 2007; Kuenzi et al. 2008).

Management of ponderosa pine forests

General restoration guidelines for ponderosa pine forests include the need to prevent large crown fires, decrease tree density and fuel load, open the forest canopy and increase herbaceous cover (Covington and Moore 1994; Fulé et al. 1997). Fuel reduction programs in ponderosa pine forests include mechanical thinning and prescribed burning in effort to decrease wildfire and crown fire potential (Hunter et al. 2006). One management response to the increase in fires outside the historical range has been an emphasis on post-fire rehabilitation and restoration. The immediate loss of vegetation leaves the land more susceptible to erosion and managers often employ treatments such as landscape scale seeding, mulching or contour felling to mitigate this effect (Robichaud et al. 2000). On Forest Service managed lands, the Burned Area Emergency Rehabilitation (BAER) team is given the task of promoting ground cover to stabilize slopes and reduce soil erosion (Robichaud et al. 2000; Keeley 2004).

Plant response to fire

The ecological structure and function of ponderosa pine forests are disturbance-driven and the understory plant communities are shaped by fire history. Low severity

fires promote heterogeneity across the landscape and consequently change the understory community composition and maintain the herbaceous diversity (Laughlin et al. 2005; Crawford et al. 2001). With the suppression of fire, there has been a decrease in species richness and herbaceous cover and consequently a strong negative correlation between pine density and understory production (Moore and Deiter 1992; Laughlin et al. 2005; Laughlin and Abella 2007; Sabo et al. 2008). Understory species richness, diversity, and cover respond positively to the increase in light and nutrient availability and decrease in litter cover that result from fire (Laughlin et al. 2004; Huisinga et al. 2005; Kuenzi et al. 2008; Stella 2009).

While researchers generally agree that fire as a disturbance creates an environment more susceptible to invasion, the ultimate conclusions vary. Some studies have shown non-native presence amplifying with increasing fire severity (Crawford et al. 2001; Griffis 2001; Barclay et al. 2004; Hunter et al. 2006) while other studies have shown no difference in non-native cover between severities or unburned sites (Huisinga et al. 2004; Kuenzi et al. 2008). The difficulty in interpreting nativity makes this discrepancy more difficult to reconcile. Crawford et al. (2001) and Barclay et al. (2004) both classify species as non-natives that would otherwise be considered native if using a more narrow definition (Huisinga et al. 2004; Kuenzi et al. 2008) of native based on the USDA/NRCS PlantsDatabase. However, in general ponderosa pine forests are relatively resilient to exotic invasions with non-native cover less than 10% even after fire (McGlone and Egan 2009).

Successional patterns and plant strategies

Theories of plant community succession are a starting point for understanding the vegetation structure resulting from a large-scale disturbance such as fire. Floristic communities are defined as species that occur together and significantly affect the distribution and abundance of each individual (Connell and Slayter 1977). Clements (1936) theorized that vegetation communities have a tendency towards stability because of succession and that they would follow strict patterns of establishment. Disturbance from a high severity fire in ponderosa pine forests is usually non-catastrophic with a mosaic of sites with varying species composition from which the barren sites are repopulated (Platt and Connell 2003). The mosaic pattern will provide residual plant populations for regeneration and restoration of the plant community in a non-linear fashion (Platt and Connell 2003). Other models suggest that perhaps the direction of plant establishment may be dictated more by life history traits (Connell and Slayter 1977; Platt and Connell 2003).

Ecosystem stability and resiliency are part of most management goals. There have been numerous competing and complementary models that attempt to explain how stability and resiliency can be achieved (Roberts and Gilliam 1995; Peterson et al. 1998). Species diversity is correlated with stability, but scale; life history traits; and frequency, size, and intensity of disturbance also affect ecosystem responses (Roberts and Gilliam 1995). The intermediate disturbance theory is often used to explain the co-existence of species. The idea revolves around the concept that the highest native diversity will occur at the intermediate disturbance regime (size, frequency, and intensity of the disturbance) (Roberts and Gilliam 1995). Species that are able to survive the disturbance will persist

and co-exist with the newly acquired species. Roberts and Gilliam (1995) suggest that at the landscape-scale, the greatest diversity will occur under the historical disturbance regime. This idea is different from the intermediate disturbance hypothesis (IDH) as it encompasses the range of size, frequency, and intensity of disturbance found in natural regimes that is in part ignored by the IDH. The IDH is based on averages of disturbance rather than ranges. Peterson et al. (1998) suggest that a relationship exists between species diversity and ecological functions in that species as individuals and in functional groups have specific ecological roles and those individuals and groups interact at different scales. Overlapping functions of species across various scales leads to a distribution of functional diversity across the landscape and leaves the ecosystem more resilient to disturbance (Peterson et al. 1998).

Grime (1977) recognizes three distinct strategies for plant growth and establishment: competitive (C-selected), stress-tolerant (S-selected) and ruderal (r-selected). Competitive plants thrive in habitats of low stress and low disturbance, and occupy the range between stress-tolerant and ruderal species. Stress-tolerant species function well in high stress habitats (shortages of light, water or nutrients) with little disturbance and are often long-lived perennials. Plants most often associated with fire prone systems are ruderal species that are well adapted to high disturbance, but low stress. Ruderals usually dedicate most of their acquired energy to reproduction and are most often annuals or biennials.

In the race to establish, early-successional plants actively compete for light and nutrients. These species are often more efficient at utilizing light at high intensities for photosynthesis (Huston and Smith 1987; Craine 2005). Other plant traits that facilitate

early invasion are the production of numerous small, easily dispersed seeds, rapid growth rate and a short life span (Grime 1977; Huston and Smith 1987).

Post-fire seeding

History of post-fire rehabilitation

In 1974, the U.S. Forest Service developed the idea of BAER teams (Robichaud et al. 2000). The overall goals after a fire are first to assess if there is an emergency situation and then plan rehabilitation for the purpose of minimizing the threat to life and property and reducing flood runoff, onsite erosion and offsite sedimentation (Robichaud et al. 2000). There are three areas to be considered for post-fire rehabilitation: hillslope, channel and road treatments (Robichaud et al. 2000). Hillslope treatments are designed to reduce runoff and maintain soil integrity and are done with contour-felled logs, application of mulch and/or grass seeding. Seed can be aurally broadcast or ground-applied by hand and may have additional fertilizer. Channel treatments involve altering the sediment and water movement to prevent or control increased surface runoff using newly installed check dams. Road treatments such as installing culverts and/or water bars are often employed to direct and control the water and sediment of road structures and other nearby surfaces.

Seeding has historically been the most common form of BAER team rehabilitation in the west (Robichaud et al. 2000; Keeley 2004). Exotic grasses and cultivars are commonly used for post-fire seeding as they are readily available, inexpensive, germinate quickly and establish in a variety of conditions providing quick vegetative cover (Robichaud et al. 2000). Although this has been common practice for

many years, it is controversial because, although the concept is sound, evidence supporting its effectiveness is lacking and the intentional introduction of exotics conflicts with other management goals (Robichaud et al. 2000; Beyers 2004; Keeley et al. 2006; Peppin et al. in review). Ryegrass, *Lolium perenne ssp. multiflorum* ((Lam.) Husnot), has historically been the predominant exotic grass used by the U.S. Forest Service and BLM BAER teams for post-fire rehabilitation (Robichaud et al. 2000; Beyers 2004). Ryegrass is often marketed as an annual or biennial and chosen with the expectation that it will exit the system within a few years of seeding (USDA/NRCS 2002). However, the fact that annual ryegrasses can cross-pollinate freely with related perennial taxa, make it difficult to maintain genetic purity especially in regards to life cycles. Ryegrass seeds sold for restoration purposes are often a mix of annual and perennial species (USDA/NRCS 2002).

Exotics species often utilize nitrogen, light and water more efficiently than native bunchgrasses (Nadkarni and Odion 1986; Conard et al. 1991; Barclay et al. 2004; Keeley 2004; Hunter and Omi 2006) giving them competitive advantages over native species. Competitively superior exotics can decrease available resources and subsequently cause a decrease in native abundance (Bescheta et al. 2003). In addition, ryegrass may compete allelopathically with native species (Taskey et al. 1989). As a result, ryegrass planted after fires may become invasive and/or displace more desirable native species (USDA NRCS 2002). Managers that use seeding to promote the long term health and sustainability of an ecosystem may produce a result contrary to that goal by intensifying competition with non-natives (Bescheta et al. 2003).

The last 30 years have seen a shift in policy and social values towards use of native species and locally adapted seed sources for revegetation instead of the traditionally used non-native-species. However, the cost and difficulty associated with collecting native seeds for large scale projects is often seen as prohibitive and managers are hesitant to invest the time and effort into obtaining native seed (Richards et al. 1998; Beyers 2004). Recently there has been an enthusiastic effort on the part of the National Park Service to not only use native seeds, but to use local genetic strains, collected on location. The Interagency Burned Area Rehabilitation Guidebook (2004) stresses that natural recovery by native plant species is the preferred method of rehabilitation and discourages the use of non-natives in re-seeding efforts. Common southwestern native grass mixes contain *Bouteloua curtipendula* [(Michx.)Torr.] (Sideoats grama), *Bromus marginatus* (Nees ex Steud.) (Mountain brome), *Elymus trachycaulus* [(Link) Gould ex Shinnery] (Slender wheatgrass), and *Schizachyrium scoparium* [(Michx.) Nash] (Little Bluestem).

Effectiveness of seeding at decreasing erosion

Because of the difficulty and expense of measuring hillslope erosion directly, easily measured estimates of ground cover are often substituted (Beyers 2004, Robichaud et al. 2000). Total ground cover including vegetation, litter, rock and wood must be at least 60% cover to protect soil from erosive forces (Robichaud et al. 2000). As a general rule, researchers have found that seeding with non-natives in ponderosa pine forests does not provide enough cover to decrease soil erosion (Peppin et al. in review). Research in the chaparral regions of California report varying results of seeding effectiveness and are often dependent on the initial cover of the seeded species. A study by Beyers et al.

(1998) reported initial low cover of *L. perenne* which subsequently did not provide enough cover the first growing season to inhibit soil erosion. Taskey et al. (1989) conducted a sediment flow study after seeding with *L. perenne* and found no significant decrease in soil erosion with seeding. A study by Stella (2009) in northern Arizona also concluded that cover of seeded species was insufficient to prevent erosion.

Seeding and exotic invasions

Post-fire seeding is often designed to control the spread of exotics (Robichaud et al. 2000; USDA BAER 2006; USDA USNF 2007). Forested landscapes that have been relatively undisturbed by fire or human impacts typically have low cover of exotics species (Huisinga et al. 2005; Keeley 2004) but when fire is introduced it opens the canopy, exposes bare mineral soil, increases soil pH, and releases phosphorous and nitrogen creating an improved habitat for exotic germination (Keeley 2004; DiTomaso et al. 2006; Floyd et al. 2006). Exotic species are often quite successful post-disturbance as their seeds are viable for long periods (Grime 1977, Korb et al. 2005). The increase in available resources subsequently leads to an overall increase in plant diversity and it is suggested that greater biodiversity and more available resources leads to greater exotic invasion (Stohlgren et al. 1999; Floyd et al. 2006).

The success of seeding with non-natives in reducing exotic cover is closely linked to the total cover of the seeded species (Peppin et al. in review). Most studies that report a decline in non-native cover also report a significant difference in cover between seeded and non-seeded sites (Barclay et al. 2005; Keeley 2004). Where seeded species achieve only low cover, no significant decrease in non-natives and no difference in total cover is

usually reported (Hunter and Omi 2006; Stella 2009). While the areas of high cover of seeded species may have fewer non-natives in one sense, when including the seeded species in the analysis, the non-native cover is high and often prohibitive to native species regeneration (Barclay et al. 2004; Keeley 2004; Peppin et al. in review).

Weed invasions after seeding with native species are not any more predictable than when seeding with non-natives. There is a strong correlation between increased species diversity and susceptibility to exotic invasions (Stohlgren et al. 1999) even when seeding with natives. Springer et al. (2004) evaluated sites that had been thinned, burned and seeded with a native mix. They found an increase in species diversity that is in part due to the fact that there were twice as many non-native species present in seeded sites. While it is difficult to pinpoint an explanation for the increase in non-natives, they propose that contaminated seed mix, increased human presence, or greater non-native presence in seedbank all play a significant role. In this case, they found no evidence that seeding with natives inhibited the invasion of exotics. In Mesa Verde National Park, Floyd et al. (2006) found that seeding with natives suppressed the spread of *Carduus nutans* (L.) but its effect was not consistent on all exotics.

Effects of seeding on native plant cover

Researchers have found that seeding with non-natives in ponderosa pine forests often negatively impacts the native vegetation (Peppin et al. in review). Seeding with non-natives often leads to a decrease in total native herbaceous cover and native species richness (Griffin 1982; Nadkarni and Odion 1986; Taskey et al. 1989; Conard et al. 1991; Barclay et al. 2004; Kruse et al. 2004). Beyers et al. (1998) reported a decrease in native

cover associated with an increase in *L. perenne* cover in the chaparral as well. The propagule pressure from non-native seeded species may decrease the ability of natives to establish by usurping the available water and nutrients (Barclay et al. 2004; Hunter et al. 2004). However, Kuenzi et al. (2008) found that when native grass and forb species were seeded in combination with wheat (*Triticum aestivum*) there were minimal negative effects from the seeded species. Wheat was present in the first year post-fire, but decreased significantly in subsequent years. Their study did not include a detailed examination of the community composition differences between seeded and non-seeded areas and hence the long term effects of seeding remain unknown. In a study done in a California forest, Keeley (2004) reported a decline in post-fire endemic forbs due to the high cover of the seeded species, *T. aestivum*.

Effects of seeding on shrubs and trees

Studies that report higher initial cover of *L. perenne* subsequently report a significant effect of the seeded species on tree and shrub seedling regeneration (Nadkarni and Odion 1986; Taskey et al. 1989; Conard et al. 1991; Barclay et al. 2004), but studies with low cover of seeded species typically report no difference in tree or shrub seedling regeneration (Beyers et al. 1998). The shrub layer in chaparral regions provides important ground cover for soil stabilization and wildlife habitat (Conard et al. 1985; Nadkarni and Odion 1986). *Ceanothus spp.* in particular were often negatively affected by seeding but responded positively to fire (Nadkarni and Odion 1986; Conard et al. 1991; Huffman and Moore 2004; Keeley 2004). These shrubs re-sprout from adventitious-bud root crowns and have seeds that are well adapted to persist in fire and are stimulated to germinate after a disturbance (Conard et al. 1985). *Chamaebatia foliolosa* (Benth)

(mountain misery) is a common shrub in the Sierra Nevada forests with similar ecological functions as *Ceanothus spp.* and was significantly reduced in areas seeded with *Triticum aestivum* (L.) (Keeley 2004).

Seeding and native plant community composition and species richness

Long-term studies are needed to fully evaluate the imprint of seeding on floristic communities but short-term studies indicate a strong correlation with successful seeding and decreased species richness (Amaranthus et al. 1993; Keeley 2004; Peppin et al. in review; Stella 2009). Studies more than 5 years post-fire and post-seeding are rare and leave a gap in the knowledge of lasting impacts of seeding on floristic composition. We do know from some studies that, at least in the short-term, seeding changes the community composition (Stella 2009). One study in northern Arizona demonstrates this difference with statistically significant differences in plant community composition and visual differences observed through ordinations where the seeded sites separate out from the non-seeded sites in species compositional space (Stella 2009). It is obvious that the community composition is different and moving along a different trajectory; deciding whether this is positive or negative depends on the ultimate restoration goals.

Future research

Long-term studies are greatly needed to determine the ultimate effects of high severity fire and post-fire seeding on the floristic composition. Researchers and managers should work together to continue monitoring study areas that have already been established as well as instigating new studies. There is also a lack of information of specific species response to fire and seeding. While the Fire Effects Information System

developed by the Rocky Mountain Research Station provides a clearinghouse for species response to fire, there are very few species with complete information (USDA FEIS 2009). Additional studies on ponderosa pine regeneration following fire and seeding would be beneficial for managers when determining if seeding is the appropriate measure for post-fire rehabilitation. Appropriate, well designed, statistical tests are difficult to set-up in burned areas but an emphasis on experimental designs that minimize the confounding effects of slope, aspect, elevation, and pre-fire vegetation differences are necessary.

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CHAPTER TWO

Effects of post-fire seeding with ryegrass (*Lolium perenne* spp. *multiflorum*) on understory plant communities

Abstract

Seeding after high severity wildfires is often done with the goals of decreasing soil erosion and preventing exotic plant invasions. We measured the vegetation response to post-fire seeding with *Lolium perenne* spp. *multiflorum* (L.) (ryegrass) in the Warm Fire in northern Arizona. We compared high severity burn areas that were seeded to those left to natural regeneration (non-seeded) and assessed the effectiveness of seeding on decreasing bare soil and increasing vegetative cover, as well as the effects of seeding on understory plant community composition, plant canopy cover, and species richness. Seeding was ineffective at decreasing bare soil and increasing vegetative cover. One year post-fire seeded areas averaged 2% ryegrass cover with a maximum of 7% and there was no significant difference in percentage of bare soil when compared to non-seeded sites. Total plant cover was not significantly different between seeded and non-seeded sites and the average cover of ryegrass was low (< 5%) 1-year post-fire. There was no difference in exotic cover between seeded and non-seeded sites. Community composition was significantly different in seeded and non-seeded plots with 15 indicator species in non-seeded and 6 indicators in seeded. We found the cover of native bunch grasses and annual and biennial forbs to be significantly lower in seeded plots when compared to non-seeded plots. Species richness did not differ between treatments. Our results add to the growing body of evidence that seeding is ineffective at significantly increasing vegetative cover,

decreasing bare soil and preventing the invasion of exotics. Furthermore, seeding is intended to restore the vegetation community and our results indicate that the observed changes in plant community may be contrary to long term ecological goals.

Introduction

The ponderosa pine (*Pinus ponderosa* var. *scopulorum* C. Lawson) forests of the American Southwest are vastly different in structure, function and ecological processes than 150 years ago (Covington and Moore 1994; Allen et al. 2002). The interactions of grazing and fire suppression have created unnaturally high levels of fuel accumulation resulting in historically uncommon large and severe crown fires (Covington and Moore 1994; Allen et al. 2002). The effects of these fires outside the historical range of variability are: increased tree mortality (McHugh and Kolb 2003), an initial decrease of understory plant cover (Springer et al. 2004; Hunter et al. 2006) and the subsequent susceptibility of the landscape to invasion of non-natives, soil erosion and flooding (Beyers 2004; Keeley 2004; Hunter et al. 2006). Many managers are responding to these fires by emphasizing post-fire rehabilitation and restoration. The immediate loss of vegetation leaves the land more susceptible to erosive forces and managers often employ treatments such as contour felling of logs, landscape-scale seeding or mulching to mitigate this effect (Robichaud et al. 2000). Seeding is the technique most often used to accomplish the objectives of controlling soil erosion and exotic plant invasions (Robichaud et al. 2000; Keeley 2004). Although this has been common practice for many years, it is controversial because evidence supporting its effectiveness is lacking and conflicts with other management goals (Robichaud et al. 2000; Beyers 2004; Keeley et al. 2006; Peppin et al. in review).

Post-fire seeding is often done with the assumption that seeding will increase plant cover and decrease exposed bare soil thus preventing soil erosion (Robichaud et al. 2000; Beyers 2004). Because of the difficulty and expense of measuring hillslope

erosion, estimations of ground cover are often substituted (Beyers 2004, Robichaud et al. 2000). As a result, many managers employ a 60% cover threshold to determine the success of post-fire seeding. This threshold can include strictly live vegetation or total ground cover including litter, rock, duff, wood, etc. (Orr 1970; Noble 1977; Robichaud et al. 2000; Beyers 2004; USDA BAER 2006). The proportion of plant and ground cover to bare soil is important in determining the amount of post-fire erosion. Increased plant cover intercepts precipitation before it hits the soil and can prevent rain-splash and sheet erosion while plant roots act to increase the rate of water infiltration (Debano et al. 1998 and Benavides-Solorio and Macdonald 2001). One study in a ponderosa pine forest in New Mexico demonstrated that as bare soil reaches a threshold of ~ 60-70% on high severity burn areas, the amount of soil erosion increases (Johansen et al. 2001). Other studies in coniferous forests reported a strong and positive relationship between 50-70% ground cover (live vegetation, litter, rock and wood) and decreased soil erosion (Benavides-Solorio and MacDonald 2001; Wagenbrenner et al. 2005).

Exotic grasses and cultivars are commonly used in post-fire seeding as they are readily available, inexpensive, germinate quickly and establish in a variety of conditions providing quick vegetative cover (Robichaud et al. 2000). *Lolium perenne ssp. multiflorum* [(Lam.) Husnot], ryegrass, is a commonly used exotic grasses for post-fire rehabilitation (Robichaud et al. 2000; Beyers 2004). Ryegrass used for post-fire seeding is an annual or biennial and chosen with the expectation that it will fail to regenerate and therefore disappear from the plant community (USDA/NRCS 2002). However, annual ryegrasses cross-pollinate freely with related perennial *Lolium* taxa and make it difficult to maintain genetic purity especially in regards to life cycles thus, ryegrass seeds used for

restoration purposes are often a mix of annual and perennial species (USDA/NRCS 2002).

Exotics species often utilize nitrogen, light and water more efficiently than native bunch grasses (Nadkarni and Odion 1986; Conard et al. 1991; Barclay et al. 2004; Keeley 2004; Hunter and Omi 2006b) giving them competitive advantages over native species. Competitively superior exotics can decrease available resources and subsequently cause a decrease in native abundance (Bescheta et al. 2003). Ryegrass has been shown to compete allelopathically with native species (Taskey et al. 1989). As a result, ryegrass planted after fires may become invasive and/or displace more desirable native species (USDA/NRCS 2002). Managers seed with the goal to promote the long term health and sustainability of an ecosystem but may produce a result contrary to that goal by intensifying competition with non-native seeded species (Beschta et al. 2003).

The impacts of post-fire seeding with exotic grasses on native plant community composition tend towards the suppression of native graminoids, forbs, shrubs and tree seedlings, but vary depending on the seeded species, method of seed dispersal, initial cover of the seeded species and post-fire precipitation (Keeley 2004; Barclay et al. 2004; Hunter and Omi 2006b; Peppin et al. in review). An inverse relationship occurs in many studies between the cover of ryegrass and the cover of natives and native species richness (Griffin 1982; Taskey et al. 1989; Beyers et al. 1998; Barclay et al. 2004; Keeley 2004). Hunter and Omi (2006a) established that native grass density was lower in seeded sites and concluded that seeded grasses were the source of propagule pressure that inhibited establishment of native grasses. Seeding has been shown to disrupt or eliminate the presence of fire-following annuals and disrupt root establishment of soil stabilizing

perennials, especially shrubs (Griffin 1982; Taskey et al. 1989; Keeley 2004; Stella 2009). In areas of high severity fire when cover of the seeded species is high (>40%), ponderosa pine seedling regeneration and survivorship may be inhibited (Griffin 1982; Barclay et al. 2004). A study on post-fire seeding in the same region as this study found that seeding decreased the cover of annual/biennial forbs, perennials and shrub species when compared to unseeded sites and these differences persisted into 2 years post-seeding (Stella 2009). All of the preceding studies were short-term investigations (less than 5 years post-fire) and the long-term significance of seeding on native vegetation remains unknown (Robichaud et al. 2000; Beyers 2004; Peppin et al. in review).

Here we report on a study on the effects of post-fire seeding with ryegrass on 4,000 ha of ponderosa pine forest located in the Warm Fire on the North Kaibab Plateau in northern Arizona (Fig. 2.1). The Warm Fire was the first large Wildland Fire Use (WFU) fire on the North Kaibab Ranger District of the Kaibab National Forest and had unintended consequences. It burned a total of 13,000 ha in the WFU portion with mixed severities and another 11,000 ha outside the management area. For this study we addressed the following hypotheses:

1. Post-fire seeding with ryegrass will provide an immediate increase in vegetation cover and decrease in bare soil to mitigate for soil erosion.
2. Ryegrass will not persist in the plant community beyond 3-years post-seeding.
3. Seeding with ryegrass will decrease the spread and invasion of exotic species.
4. Seeding with ryegrass will lead to a decline in native herbaceous cover and overstory regeneration.

5. Seeding with ryegrass will alter the plant community composition and decrease species richness.

Methods

Study Area

The study sites are located in the Warm Fire on the Kaibab Plateau in the Kaibab National Forest in northern Arizona, USA (Fig. 2.1). Plot locations range in elevation from 2300 to 2590 m and at the landscape-scale have a similar disturbance history in terms of grazing and logging (Trudeau 2006). The fire burned across three vegetation communities: higher elevation mixed conifer (white fir (*Abies concolor* (Gordon and Glendinning) Hoopes), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) and blue spruce (*Picea pungens* Engelm.); mid-elevation ponderosa pine dominated interspersed with quaking aspen (*Populus tremuloides* Michx.), and Gambel oak (*Quercus gambelii* Nutt.) and lower elevation pinyon-juniper woodlands [*Pinus edulis* Engelm., *Juniperus osteosperma* Torr.] (USDA USNF 2007). This study was conducted in ponderosa pine dominated overstory with an understory composed of common grasses, such as muttongrass (*Poa fendleriana* (Steud.) Vasey), squirreltail (*Elymus elymoides* (Raf.) Swezey), and Junegrass (*Koeleria macrantha* (Ledeb.) Schult) and common forbs including small leaf pussytoes (*Antennaria parvifolia* Nutt.), Fendler's sandwort (*Arenaria fendleri* A. Gray), and woolly cinquefoil (*Potentilla hippiana* Lehm.).

The 14-year average annual precipitation was 61cm between 1995 and 2010. Roughly half of the precipitation comes during winter months in the form of snow while the remainder falls during summer monsoon rainstorms. Annual precipitation for the

years covered by this study was 48 cm in 2007, 33 cm in 2008, 30 cm in 2009 (measured from October-September; Fig. 2.2). Precipitation in May and June of 2009 was unusually high whereas precipitation in July and August was lower than average. This may have influenced the number of annual and biennial forbs we recorded in 2009 as we may have missed some species that bloomed earlier than usual due to the increased early precipitation. Temperatures range from an average January minimum of -5.7 °C and an average July maximum of 26.1 °C (Western Regional Climate Center, 2009). Soils are derived from Kaibab Limestone parent material (Brewer et al. 1991).

Moderate and high severity burn areas of the wildfire section were seeded with ryegrass for the purpose of reducing flood risk, soil erosion, and invasion of non-native plant species (USDA BAER 2006). Across the landscape, 4,063 ha of ponderosa pine and mixed conifer forests were seeded with ryegrass at a rate of 3.92 kg/ha⁻¹. Certified weed-free seed was applied by fixed wing aircraft in the first week of July (USDA BAER 2006). Summer monsoonal rains began within a week of seeding and washed the majority of the seed into the drainages (USDA USNF 2007). Some germination of ryegrass occurred but it was not consistent across the landscape with more seed in drainages and areas of low slope than on the steeper slopes (USDA USNF 2007).

Sampling design

Our study took advantage of a random disturbance (wildfire) and therefore we were unable to employ a more robust sampling design including replication and randomization (van Mantgem et al. 2001). Plots were stratified by fire severity, elevation, vegetation, slope, soils and BAER treatment. Sample points were randomly selected

within strata using ArcView GIS software (ESRI 2006). High severity areas were delineated using the BAER burn severity map derived from Landsat satellite imagery and ground-truthed using the Composite Burn Index (Key and Benson 2006). Site elevation was restricted to within the ponderosa pine vegetation type on slopes less than 28°. Soils were determined using Terrestrial Ecosystem Survey of the North Kaibab National Forest layers and were restricted to Mollic Eutroboralfs (Brewer et al. 1991). Non-seeded sites were scattered across the fire in areas not subjected to post-fire rehabilitation (seeding) while seeded sites were restricted to the wildfire section (Fig. 2.1). The southern portion of the fire burned more consistently as a crown fire and was classified as a wildland fire receiving rehabilitation (suppression and seeding) treatments while the northern portion of the fire burned in a mosaic of fire severities. We controlled for environmental variation as much as possible, but the seeded sites are located in a different part of the forest; more consistently along exposed ridges when compared to non-seeded sites.

In 2007, as a pilot study one year post-fire, 7 plots in each treatment were permanently established (n=14) and measured for 3 years. We added 15 plots to each treatment in 2008 and sampled a total of 44 plots in 2008 and 2009. We sampled understory plant cover, species richness, and species composition during August and early September to capture plants at the greatest production. Understory plant cover hereafter refers to foliar cover of herbaceous plants, shrubs and tree seedlings.

Species were classified into four life habits: annual/biennial graminoids (grasses and sedges), perennial graminoids, annual and biennial forbs, perennial forbs, shrubs and trees. Plots were circular with a 7.32 m radius and six transect lines along which nine 1x1 m subplots were placed for all understory vegetation sampling (Fig. 2.3). Foliar

cover of vegetation was estimated by botanists and calibrated for consistency in each quadrat by species, life form (graminoids, forbs) and total vegetation cover. Species richness was determined for the entire plot. Tree seedling density was recorded in a 3.6 m radius sub-plot. Species were classified on the generic or family level when vegetative characteristics were insufficient to identify at the species level. Plant nomenclature and nativity are based on USDA-NRCS (2009) and voucher specimens are located in the Deaver Herbarium in Flagstaff, Arizona.

We measured forest floor cover by estimating cover of bare soil, rock, wood, litter, duff, lichen, moss, and scat at each of the nine subplots. Overstory canopy cover was measured with a densitometer in 2009 by counting the number of overstory hits at 33 points along the transect lines. Topographic variables recorded at each site were slope (degrees), aspect, and elevation (m).

Statistical analyses

We analyzed all vegetation data using a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001; McCune and Mefford PC-ORD 5.1), which is a non-parametric test that can be used with non-normal univariate or multivariate datasets. We conducted one-way analysis using Bray-Curtis distance measures for multivariate data and Euclidean distance for univariate data using 9999 permutations, with significance at $\alpha = 0.05$. Differences in species richness were determined by the total number of species per plot per year in each treatment. Species that occurred in less than 5% of the plots were omitted from species composition analysis and ordinations but included in species richness and univariate analysis (McCune and Grace 2002). To

specifically test if the seeded plots differed from the non-seeded plots in the rate of community change we used PC-ORD to calculate the Bray-Curtis distance for each plot. This method is similar to calculating the difference between two values in a paired t-test. This dissimilarity was analyzed with a PERMANOVA using Euclidean distance.

Non-metric multidimensional scaling (NMDS) was used to visualize the differences in plant community composition between seeded and non-seeded sites. Ordinations were done with PC-ORD V 5.1 (McCune and Mefford 1999) using Bray-Curtis distance measures with 250 runs with real data and 250 runs with randomizations, a maximum of 400 iterations per run and an instability criterion of .00001. Three dimensions were always recommended, however we chose the two axes that represented the most variation to create 2-D representations. We used Pearson's correlation coefficients to determine which species and covariates were most closely associated with the axes of the ordinations.

When differences in plant composition were identified in PERMANOVA analyses, we ran an indicator species analysis (ISA) to determine which species were driving those differences (McCune and Mefford 1999, PC-ORD V 5.1). ISA takes into account both relative abundance and relative frequency. Species with an indicator value > 30 and $p > 0.05$ were identified as indicator species (Dufrene and Legendre 1997).

Results

Ryegrass, bare soil and total ground cover

One year post-seeding, foliar cover of ryegrass averaged 1.5%, but individual plots ranged in cover from 0.05 - 7 %. By 2008 average ryegrass cover per plot had

decreased slightly to 1.3% with individual plots ranging from 0.05 - 13% and in 2009 the average cover dropped to 0.5% with individual plots ranging from 0.05-3%. This decrease in cover was not significantly different from previous years ($p=0.0738$). Average total plant cover (all species) in 2007 was 13% on seeded plots and 17% on non-seeded. Total cover in 2008 was 18% in seeded plots and 22% in non-seeded, and in 2009 there was an increase to 20% in seeded and 23% in non-seeded but there were no significant differences between treatments in any year (Table 2.1, Fig. 2.4).

One year post-fire bare soil averaged 23% in non-seeded sites and 34% in seeded sites and was not significantly different. Percentage of bare soil continued to decline in 2008 and 2009 in both treatments (Fig. 2.5). Total ground cover including live vegetation, litter, duff, wood, and rock was significantly less in seeded sites (27%) than non-seeded (59%) (Fig. 2.5) and in seeded sites was below the 60% threshold for significantly decreased soil erosion. By 2008 ground cover for both seeded and non-seeded sites was well above 60%, resulting in less soil erosion (Fig. 2.5).

Exotic cover

The average foliar cover of exotic species was low in all years, < 2% for non-seeded plots, < 1.0% for seeded plots and < 10% for all individual plots. The average cover was not significantly different between treatments in both 2008 and 2009 (Table 2.1). One justification for seeding was that it would inhibit the spread and establishment of exotic plants and particularly cheatgrass (*Bromus tectorum* L.) and musk thistle (*Carduus nutans* L.). Cheatgrass was present in trace amounts on two plots in 2007 but by 2008 its presence was more frequent and abundant in non-seeded sites and cover was

significantly higher in non-seeded than seeded sites (Table 2.1). In 2009, it was an indicator of non-seeded sites but this time foliar cover was not significantly different from seeded sites (Tables 2.1 and 2.2). Musk thistle was found on one non-seeded plot and two other large populations were noted nearby.

Dandelion (*Taraxacum officinale* F.H.Wigg) and common mullein (*Verbascum thapsus* Bertol.) were both indicators of non-seeded plots (Table 2.2). Yellow salsify (*Tragopogon dubius* Scop.) was present in all treatments, but an indicator of seeded sites in 2009 only (Table 2.2). Other exotics that were present in more than 5% of the plots but not significantly present in either treatment were two grass species previously seeded as forage, orchardgrass (*Dactylis glomerata* L.) and intermediate wheatgrass (*Thinopyrum intermedium* [(Host) Barkworth and D.R. Dewey] and prickly lettuce (*Lactuca serriola* L.) a non-native forb in the Asteraceae family. The presence of timothy grass (*Phleum pratense* L.) and Kentucky bluegrass (*Poa pratensis* L.) was also noted but in less than 5% of all plots.

Native cover

We tested for differences in vegetative cover based on life forms, life history and specific family characteristics. Results showed a significant difference in life forms (grass, forbs, shrubs and trees) between seeded and non-seeded in 2008 and 2009, but individual comparisons indicated that the difference was driven by the presence of trees in 2008 and 2009 and by graminoids in 2009 (Table 2.1, Fig. 2.6). When grouped by life history (annuals/ biennials and perennials), there was significantly greater cover of annuals/biennial forbs in non-seeded than seeded sites in 2008 (Table 2.1, Fig. 2.7).

There was no significant difference in leguminous cover between treatments in either year (Table 2.1).

Graminoid cover was significantly different in 2009 only (Fig.2.8).

Comparisons between graminoids showed no difference for upland sedge species (*Carex spp.*) in either year, but significantly greater cover of mountain muhly (*Muhlenbergia montana* [(Nutt.) Hitchc] in non-seeded sites both years. Muttongrass, squirreltail and Junegrass had significantly greater cover in non-seeded sites in 2009.

Ponderosa pine seedlings were an indicator species in non-seeded sites for both years and the number of seedlings was significantly different between treatments in 2008 (Table 2.1 & 2.2). Three years post-fire seedlings were present in 14 non-seeded plots and only 5 seeded plots.

Community composition and species richness

One year post-seeding total vegetative cover was low and there was no significant difference in community composition between seeded and non-seeded sites. By 2008 the plant communities significantly differed and this trend continued in 2009 ($p=0.0002$ and 0.0014 , respectively). The NMDS ordinations confirm this and show a spatial separation in data between treatments in both years (Fig. 2.9). Analysis of rate of species composition change was not significantly different between 2008 and 2009 ($p=0.4132$), thus the floristic composition was changing at a relatively consistent rate in both treatments. Species richness was not different between treatments and averaged 29 species in both treatments in 2008 and 32 species in seeded and 33 species in non-seeded plots in 2009 (Table 2.1).

Indicator species analysis identified several species strongly associated with treatments in both years. Twelve species were listed as indicators for non-seeded plots in 2008 with the notable presence of two tree species: ponderosa pine and quaking aspen; two common non-invasive exotics: dandelion and mullein; and one invasive exotic: cheatgrass. Significant species in the seeded plots were two legumes: Wright's deervetch (*Lotus wrightii* (A. Gray) Greene) and crescent milkvetch (*Astragalus amphioxys* A.Gray); one shrub; New Mexico locust (*Robinia neomexicana* A.Gray) and the seeded species, ryegrass (Table 2.2). In 2009 fourteen species were closely associated with non-seeded sites with the same species listed above and the addition of three native bunchgrasses: muttongrass, squirreltail, and mountain muhly. Seeded plots maintained the same species and added two more: horseweed (*Conyza canadensis* (L.) Cronquist) and the exotic invasive yellow salsify (Table 2.2).

Discussion

Ryegrass, bare soil and total ground cover

Post-fire seeding in the Warm Fire did not generate adequate vegetative cover to mitigate for erosion or exotic invasion. One year post-fire our seeded plots had only 13% vegetative cover and less than 2% of that was the seeded species. Seeded plots had a higher percentage of bare soil than non-seeded and cover was less than the 60-70% threshold for significantly increased erosion two years after the fire. Total ground cover was not sufficient on seeded sites one year post-fire to control soil movement. Stella (2009) found similar results for the Warm Fire one year post-fire where the percentage of bare soil was still within the danger zone of significant sediment loss and seeding

treatments did not provide adequate cover for erosion mitigation. Unfortunately, seeding as a post-fire rehabilitation method often has little or no effect on increasing ground cover or decreasing sediment yields (Johansen et al. 2001; Wagenbrenner et al. 2006; Peppin et al. in review). Successful post-fire seeding is particularly difficult in the Southwest where high intensity, short duration summer monsoon rainstorms are the norm and the majority of seed washes off slopes before they are able to germinate and establish (Robichaud et al. 2000), and this is precisely what happened in the Warm Fire (USDA USNF 2007).

Three years post-fire, ryegrass has not left the ecosystem. Because ryegrass is an annual, we predicted that it would exit the system within 3 years post-seeding. However although the cover was low, it was still present and ranged from 0.01- 5.0 %. Any space occupied by a plant is limiting the amount of nutrients, light and water for other potential species and when that space is occupied with a non-native grass species, it may preclude the establishment of other native species. As discussed previously, ryegrass is able to utilize nitrogen and light more quickly (Hunter and Omi 2006b) and may have allelopathic properties (Barclay et al. 2004) both of which could enhance ryegrass establishment and persistence and alter native species establishment.

Exotic cover

Seeding was no more effective at controlling the spread and establishment of exotics than natural recovery. Peppin et al. (in review) reported that 60% of the reviewed studies indicated seeding was ineffective at controlling exotics, mostly due to inadequate

cover of the seeded species. Our results were consistent whether the data were analyzed including ryegrass as an exotic.

The rehabilitation/seeding efforts focused on two species of potential concern; cheatgrass and musk thistle and particularly their potential impact on a sensitive cactus species- Kaibab pincushion cactus (*Pediocactus paradinei* B.W. Benson). Cheatgrass is a winter annual and a well-known invasive as it quickly permeates disturbed ecosystems displacing natives and altering fire regimes (Brooks et al. 2004). While this species is of great concern in lower elevation forests and deserts, its ability to persist in ponderosa pine forests and alter the fire regime is unknown (McGlone and Egan 2009). Studies in other Southwest ponderosa pine forests have found that even in higher elevation forests, once an area has been disturbed and cheatgrass is able to establish a presence, the subsequent disturbances act as instigators to increased invasion (Floyd et al. 2006 McGlone et al. 2009). In our study, the presence of cheatgrass in both seeded and non-seeded plots has increased from 43% of all plots to 50% in 2009. Cheatgrass cover is low (< 2%) but the observed increase warrants concern and continued monitoring is strongly recommended. We found musk thistle present on one plot and observed a substantial population at one other location in the fire. Forest managers are particularly concerned with the potential spread of musk thistle as it has the ability to rapidly invade and persist.

Native cover

Native bunchgrass regeneration may be inhibited by the pressure exerted from ryegrass presence. These grasses (squirreltail, mountain muhly and muttongrass) are well adapted to the historical fire regime and generally respond positively to low severity fires,

surface fires (Laughlin et al. 2005; Hunter and Omi 2006b) and in our study, to high severity fire as well. With these grass species as indicators of non-seeded sites, continued monitoring is needed to determine the impacts on the trajectory of native bunchgrasses in the seeded area. This ecosystem was historically dominated by bunchgrasses and a shift away from that historical landscape is inconsistent with restoration goals.

The presence of ryegrass was associated with reduced cover of annual and biennial forbs. These species are important post-fire colonizers that take advantage of the recently exposed soil, flush of nutrients, increased light and are adapted to high disturbance (Grime 1977). In non-seeded sites, these species are a significant component of the floristic community representing approximately one quarter of the total plant cover which is consistent with other studies (Laughlin et al. 2004; Stella 2009). Reference sites of ponderosa pine forests that have continued under the historical fire regime on the North Rim of Grand Canyon National Park have higher annual and biennial forb species richness and this may be an indicator of forest health (Laughlin et al. 2004). Laughlin and Fulé (2008) supported the importance of annuals/biennials in the post-fire landscape when they found annuals and biennials to be the driving force in an increase in species richness and changes in community composition after a fire.

Other studies have shown that higher cover of ryegrass (usually > 40%) inhibits the regeneration and establishment of trees and shrubs (Griffin 1982; Conard et al. 1991; Barclay et al. 2004). Ponderosa pine seedlings were an indicator species for non-seeded sites in our study and seedlings were present in more non-seeded than seeded sites, but the difference was not significant. The lack of statistical significance is in part due to the fact that ISA takes into account both abundance and frequency whereas PERMANOVA

is mostly a function of abundance. While seedling frequency was different between treatments, abundance was not. We looked for relationships between cover of ryegrass, environmental variables (slope, aspect, and litter cover) and seedlings and found no strong associations, in part because of the high variability of the data. On the plot level, there was no consistency in the presence of nearby seed trees and seedling establishment for either seeded or non-seeded plots, but we observed significant rodent activity on one seeded plot that had more than 10 ponderosa seedlings.

Community composition and species richness

The floristic composition is significantly different between treatments and they are changing at similar rates but in different trajectories. The initial seed cover was low, especially on steeper slopes, but the persistent presence of a non-native species occupies species space and limits available nutrients and water. Many of the post-fire colonizers found in ponderosa pine forests are adapted to conditions of high disturbance and the added stress of the presence of ryegrass could preclude those species from establishing (Grime 1977). A similar study, also conducted in the Warm Fire reported parallel results of persistent community differences in areas seeded with ryegrass at relatively low cover (<10%) (Stella 2009). Other researchers in different landscapes have also observed these altered communities as a result of seeding with ryegrass (Conard et al. 1991; Barclay et al. 2004) but without long-term monitoring, it is impossible to predict the lasting impacts (Robichaud et al. 2000; Beyers 2004; Peppin et al. in review). Our analysis of the rate of community change indicates that these communities are changing at similar rates, and potentially in different directions as per our indicator species analysis.

While the initial response to surface fires is a decrease in herbaceous production, the changes created by the disturbance are necessary for maintaining species diversity and richness (Moore and Deiter 1992; Laughlin and Abella 2007). Richness is thought to be greatest in an intermediate disturbance regime; one which allows for new species to colonize but does not completely remove the original suite of species. Laughlin and Fulé (2008) suggest that low severity fires are optimal for species richness and that more severe fires may result in a loss of species, predominately due to loss of duff. In our study, species richness does not appear to be negatively influenced by high severity fire but this may be the result of the mosaic of severities across the landscape and an unnatural accumulation of litter and duff before the fire. In another study (see Chapter 3), we noted significantly higher species richness in both high (non-seeded) and low severity plots when compared to unburned plots. Species richness is often determined by presence or absence of a dominant species and in our case, ryegrass was not a consistently dominant species on all plots and therefore did not inhibit species richness. Other studies that report a decrease in species richness also report higher cover (> 20%) of seeded species (Taskey et al. 1989; Conard et al. 1991; Keeley 2004).

Conclusions

A recent review of post-fire published seeding studies by Peppin et al. (in review) concludes that while seeding is a common choice, evidence supporting the effectiveness at providing adequate ground cover, decreasing bare soil and preventing exotic invasion are not well supported. Our study supports this review in all three aspects.

Post-fire seeding has been shown to negatively affect plant communities and may contradict the ultimate goal of creating and maintaining ecologically stable and diverse ecosystems (Beschta et al. 2003; Barclay et al. 2004; Stella 2009; Peppin et al. in review). Using a replicated experimental design, Stella (2009) found significant and persistent differences in the understory plant community in the Warm Fire two years after the seeding. Annual and biennial forbs that typically respond rapidly to fire decreased in abundance with the presence of seeded species (Keeley 2004; Stella 2009). Other studies have shown negative effects on native shrubs and conifer regeneration as a result of seeding (Tasky et al. 1989; Barclay et al. 2004). The conflict of seeding comes from the fact that success is determined by substantial cover of the seeded species to reduce bare soil and prevent exotic invasions but dominance of a single species has been shown to decrease the abundance of other, perhaps desirable species (Stohlgren et al. 2003; Keeley 2004).

The maintenance and rehabilitation of threatened watersheds is an important component of post-fire treatments, but seeding has not shown to be effective at increasing vegetation cover, decreasing bare soil and preventing exotic invasion (Robichaud et al. 2000; Beyers 2004; Peppin et al. in review). The results of this study add to that growing body of evidence that seeding is often not successful and may have unintended ecological consequences.

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Tables and Figures

Table 2.1. A summary of richness and actual cover values averaged for all plots within a treatment for both years. Numbers represent foliar cover of herbaceous species, shrubs and trees unless otherwise noted. Species richness is the average number of species in the treatment. Asterisks (*) indicate a significant difference ($p < 0.05$) between non-seeded and seeded plots in 2008 and 2009.

Category	2008		2009	
	Non-seeded	Seeded	Non-seeded	Seeded
Community composition				
Richness	21.68	17.63	22.09	18.53
Vegetative cover (%)	1.620	0.229	1.484	0.534
Total cover	20.10	15.91	21.59	19.03
Exotic				
Native	2.68	2.30	4.28*	2.79*
Functional groups (%)	14.96	10.17	13.18	8.91
Graminoids	2.09	3.35	3.19	4.89
Forbs	0.15*	0.02*	0.23*	0.02*
Shrubs	6.35	15.06	4.20	2.81
Trees	15.27	2.48	18.99	17.42
Annual/Biennial	3.23	3.18	2.98	2.00
Perennial				
Legumes	29	29	33	32
Species (%)				
<i>Bromus tectorum</i>	0.64*	0.03*	0.05	0.01
<i>Carex spp.</i>	0.61	0.59	1.00	0.91
<i>Elymus elymoides</i>	0.22	0.10	0.41*	0.05*
<i>Koeleria macrantha</i>	0.04	0.003	0.03	0.0002
<i>Lolium perenne</i>	-	1.35	-	0.51
<i>Muhlenbergia montana</i>	0.04*	0*	0.03*	0.00*
<i>Pinus ponderosa</i> (# plots)	14*	2*	14	4
<i>Poa fendleriana</i>	0.67	0.37	1.57*	0.77*
Abiotic variables (%)				
Litter	32.96*	18.58*	45.96*	28.84*
Rock	16.45*	33.34*	13.39*	25.48*
Soil	20.36	29.41	9.05*	19.08*

Table 2.2. Indicator species for 2008 and 2009. Only species which were significant indicators (IV > 30, p < 0.05) are listed in this table.

Treatment	Species	IV 2008	IV 2009	Life history	Life form
Non-seeded	<i>Antennaria parvifolia</i>	45.4	66.1	P	F
	<i>Androsace septentrionalis</i>	41.4	-	A	F
	<i>Arenaria lanuginosa ssp. saxosa</i>	40.8	48.5	P	F
	<i>Bromus tectorum*</i>	56.9	61.4	A	G
	<i>Chenopodium fremontii</i>	79.1	67.6	A	F
	<i>Elymus elymoides</i>	-	76.5	P	G
	<i>Hieracium fendleri</i>	33.7	38.9	B	F
	<i>Lupinus argenteus</i>	-	57.0	P	F
	<i>Muhlenbergia montana</i>	-	31.8	P	G
	<i>Packera multilobata</i>	63.8	71.7	A/P	F
	<i>Poa fendleriana</i>	-	66.8	P	G
	<i>Pinus ponderosa</i>	56.0	53.5	P	T
	<i>Populus tremuloides</i>	52.6	72.0	P	T
	<i>Pseudognaphalium macounii</i>	59.9	-	B	F
	<i>Taraxacum officinale*</i>	61.6	70.9	A/B	F
<i>Verbascum thapsus*</i>	36.4	40.9	B	F	
Seeded	<i>Astragalus amphioxys</i>	61.3	-	P	F
	<i>Conyza canadensis</i>	-	58.7	A	F
	<i>Erigeron divergens</i>	-	86.0	B	F
	<i>Hymenopappus filifolius</i>	-	39.9	P	F
	<i>Lolium perenne ssp. multiflorum*</i>	98.5	99.5	A/B/P	G
	<i>Lotus wrightii</i>	75.0	58.0	P	F
	<i>Robinia neomexicana</i>	57.0	59.1	P	S
<i>Tragopogon dubius*</i>	-	46.9	A/B	F	

* = exotic; P= Perennial, A= Annual, B= Biennial, G= Grass, F= Forb, S= Shrub, T= Tree

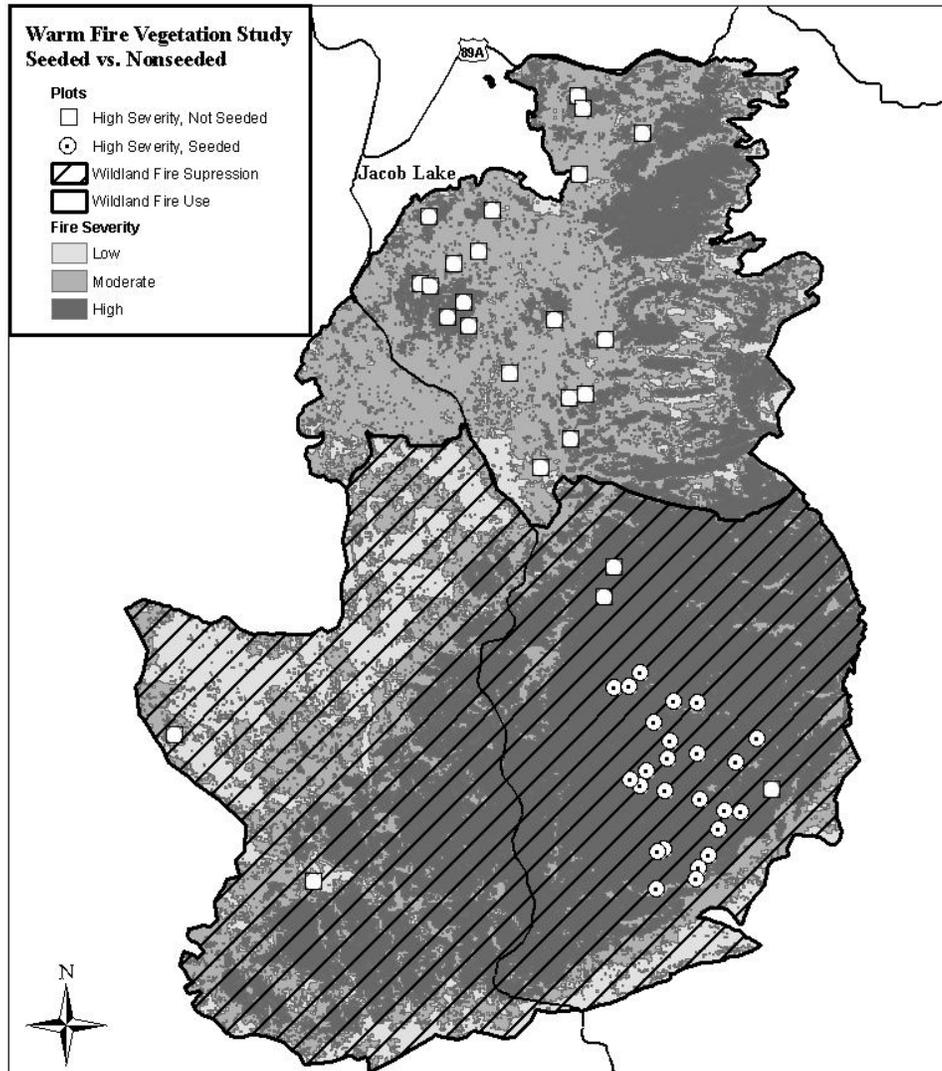


Figure 2.1. Location of study site. Perimeter of the Warm Fire; the northern portion of the fire (no crosshatch) was managed as a WFU while the southern portion (crosshatched) was managed as a wildfire and was subjected to post-fire mitigation. The fire encompassed 24,000 ha across three vegetation types. Burn severity is indicated by varying shades of grey. Seeded plots are indicated by circles and non-seeded plots by squares.

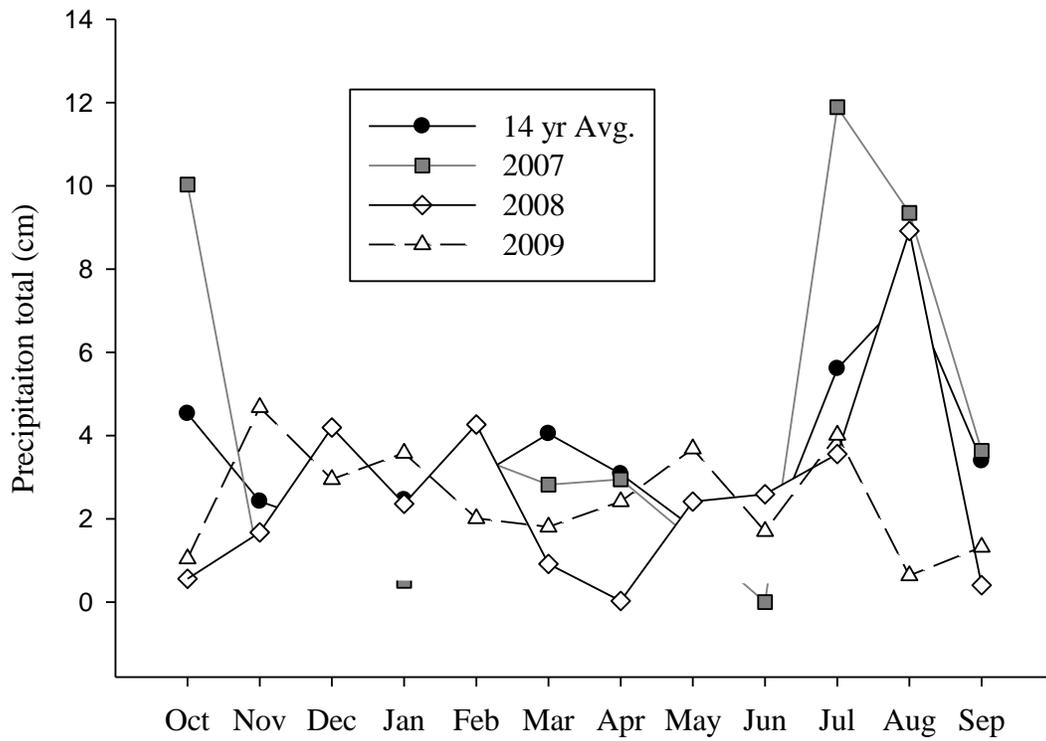


Figure 2.2 14-year average and monthly precipitation for sites during sampling years. Precipitation data was collected at the Warm Springs Canyon weather station (36° 42' 00" 112° 13' 48") at 2441 m elevation.

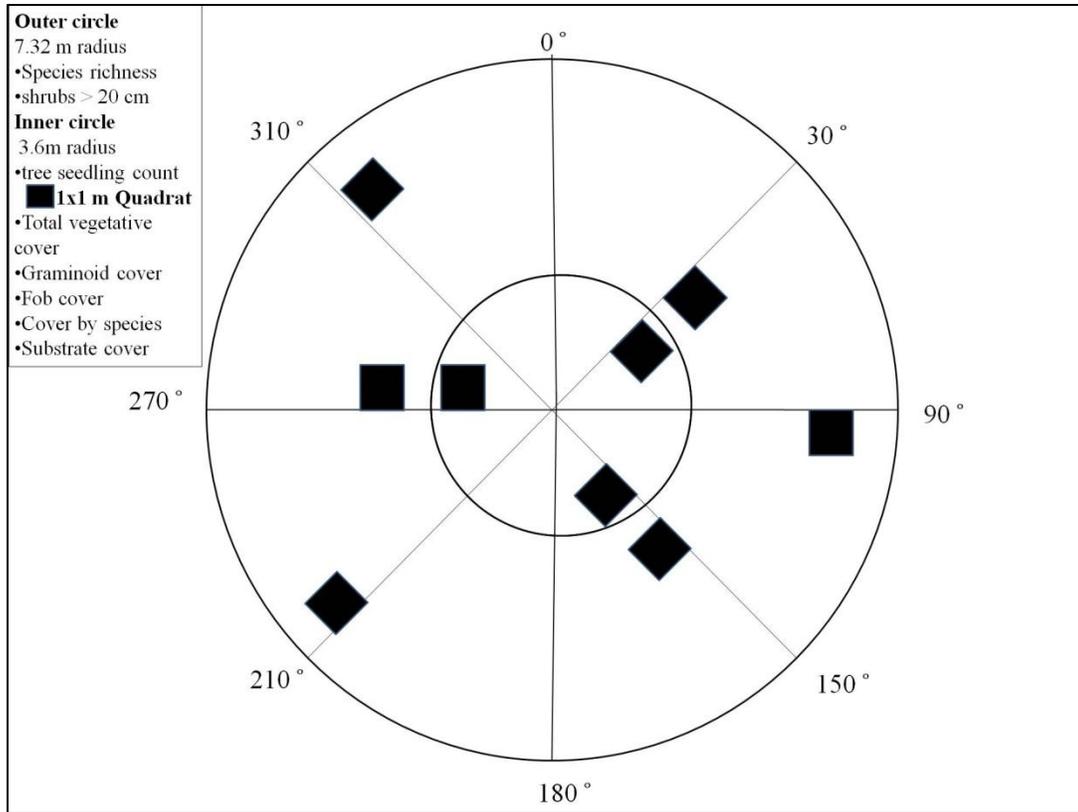


Figure 2.3. Plot layout. Species richness and shrub counts were collected from the entire circle. Nine 1x1 m quadrat frames were used to collect vegetative and substrate cover data. A smaller sub-plot in the center was used to count tree seedlings.

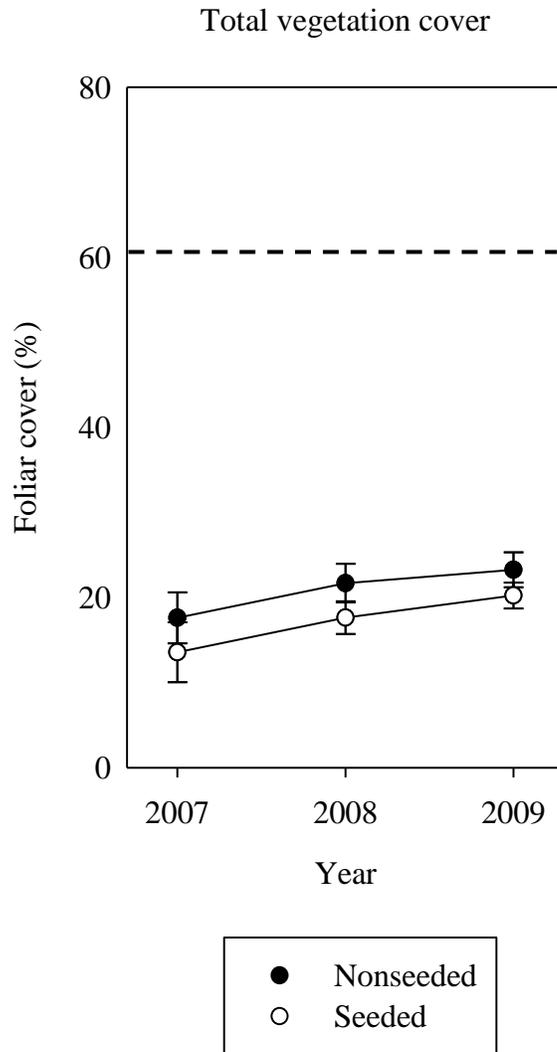


Figure 2.4. Average total vegetative cover (%) of all species by treatment and year; the dashed line represents the target cover of 60% that is associated with a lower risk of erosion runoff (Robichaud et al. 2000). There was no significant difference between treatments. Vertical bars represent +/- 1 standard error.

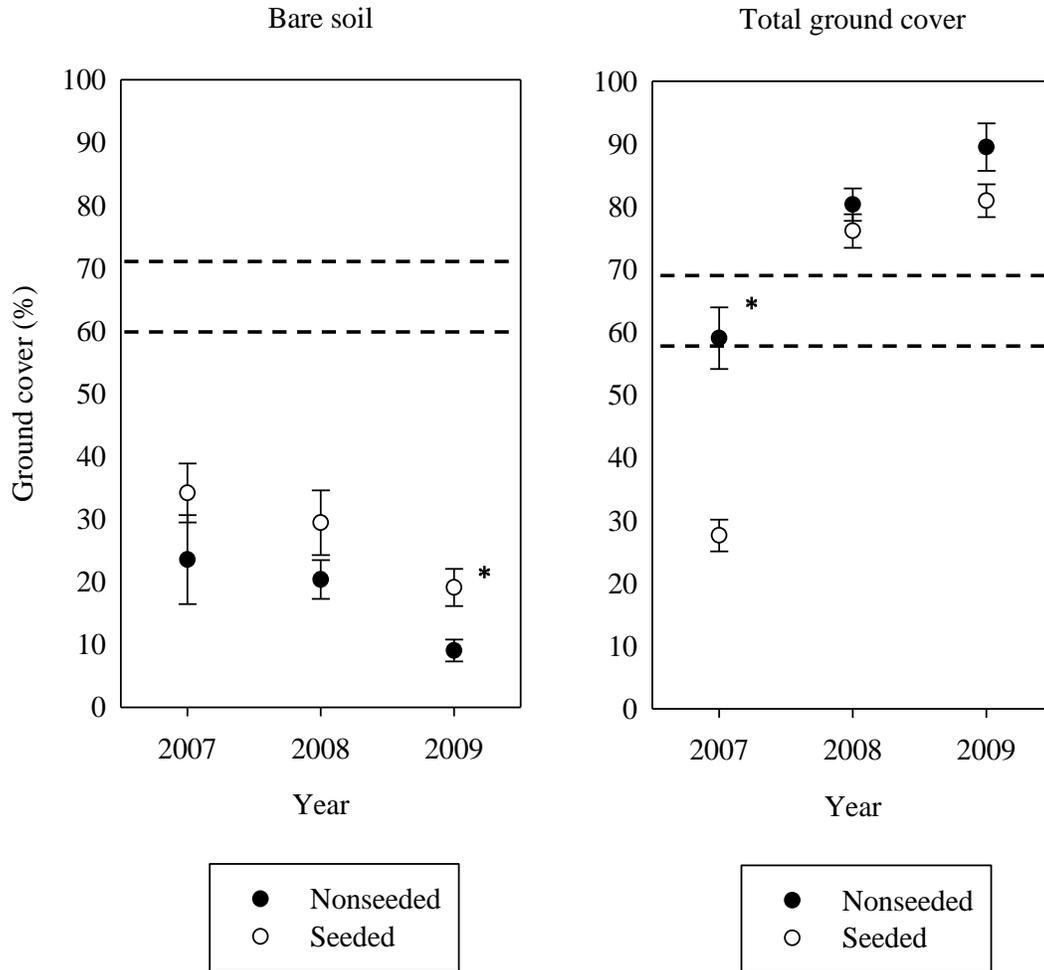


Figure 2.5. Average cover (%) of bare soil and all ground cover including litter, duff, rock, wood and vegetation in all three years in both treatments; the area between the dashed lines indicate the cover values at which erosion and runoff significantly increase for bare soil cover and decrease for total cover (Robichaud et al. 2000; Johansen et al. 2001). Asterisks (*) indicate significant difference at $p < 0.05$. Vertical bars represent ± 1 standard error.

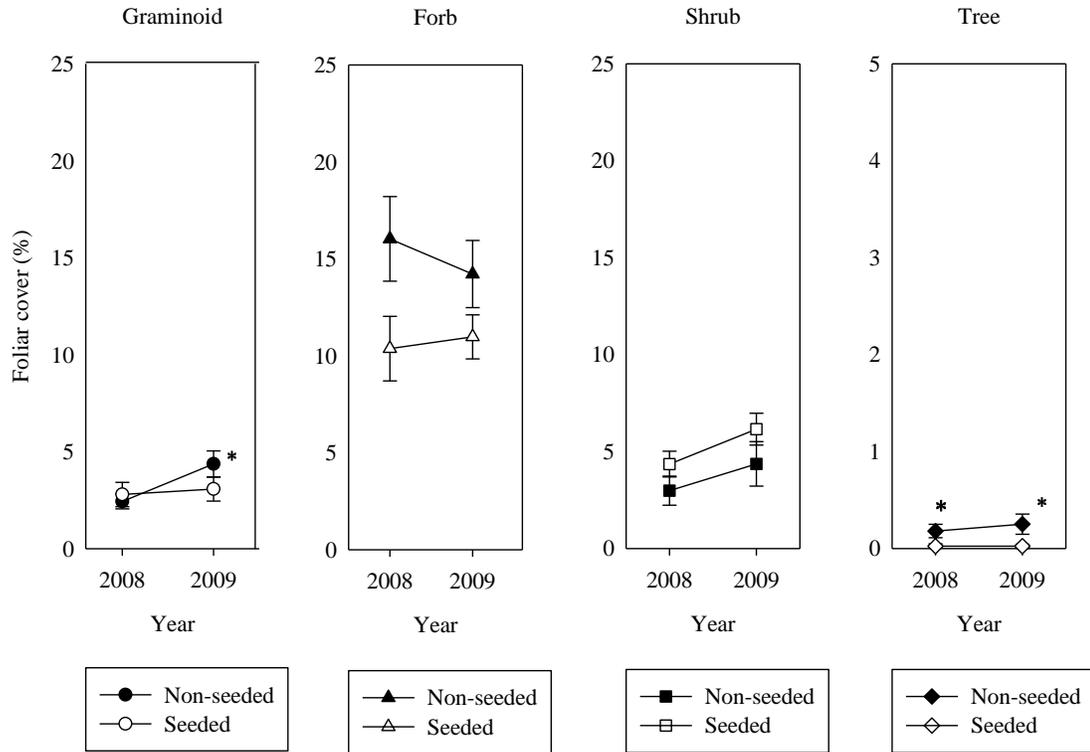


Figure 2.6. Average cover (%) of graminoids, forbs, shrubs and trees by treatment and year. Asterisks (*) represent significance at the $p < 0.05$ level. Vertical bars represent ± 1 standard error.

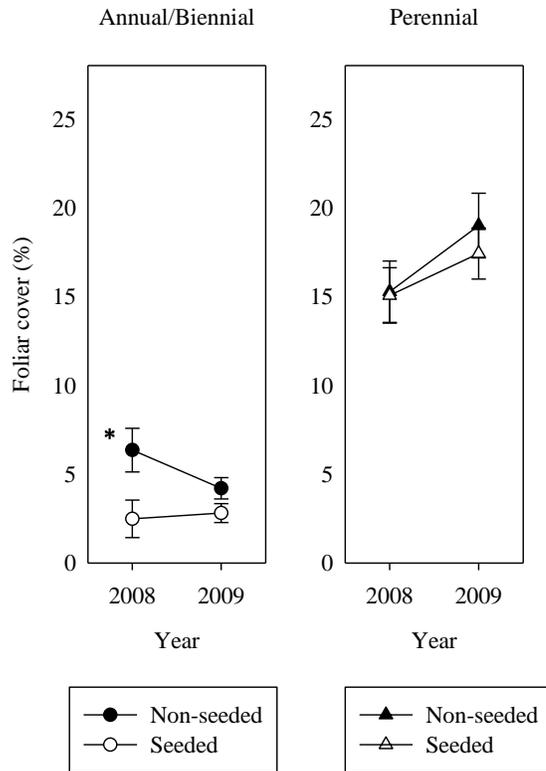


Figure 2.7. Average cover (%) of species by life history: annual/biennial and perennial. Asterisks (*) indicate significant difference at $p < 0.05$. Vertical bars represent ± 1 standard error.

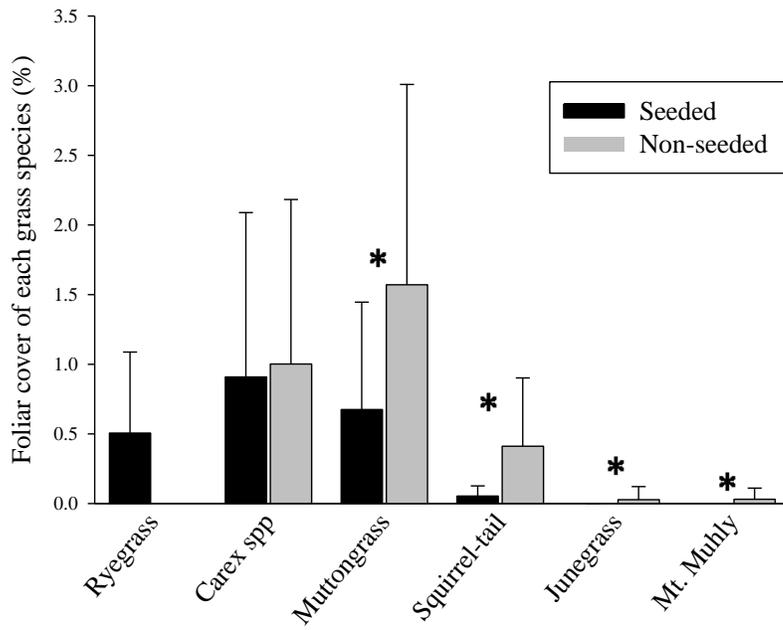


Figure 2.8. Average foliar cover of graminoid species in 2009. Asterisks (*) indicate significance at $p < 0.05$. Vertical bars represent ± 1 standard error.

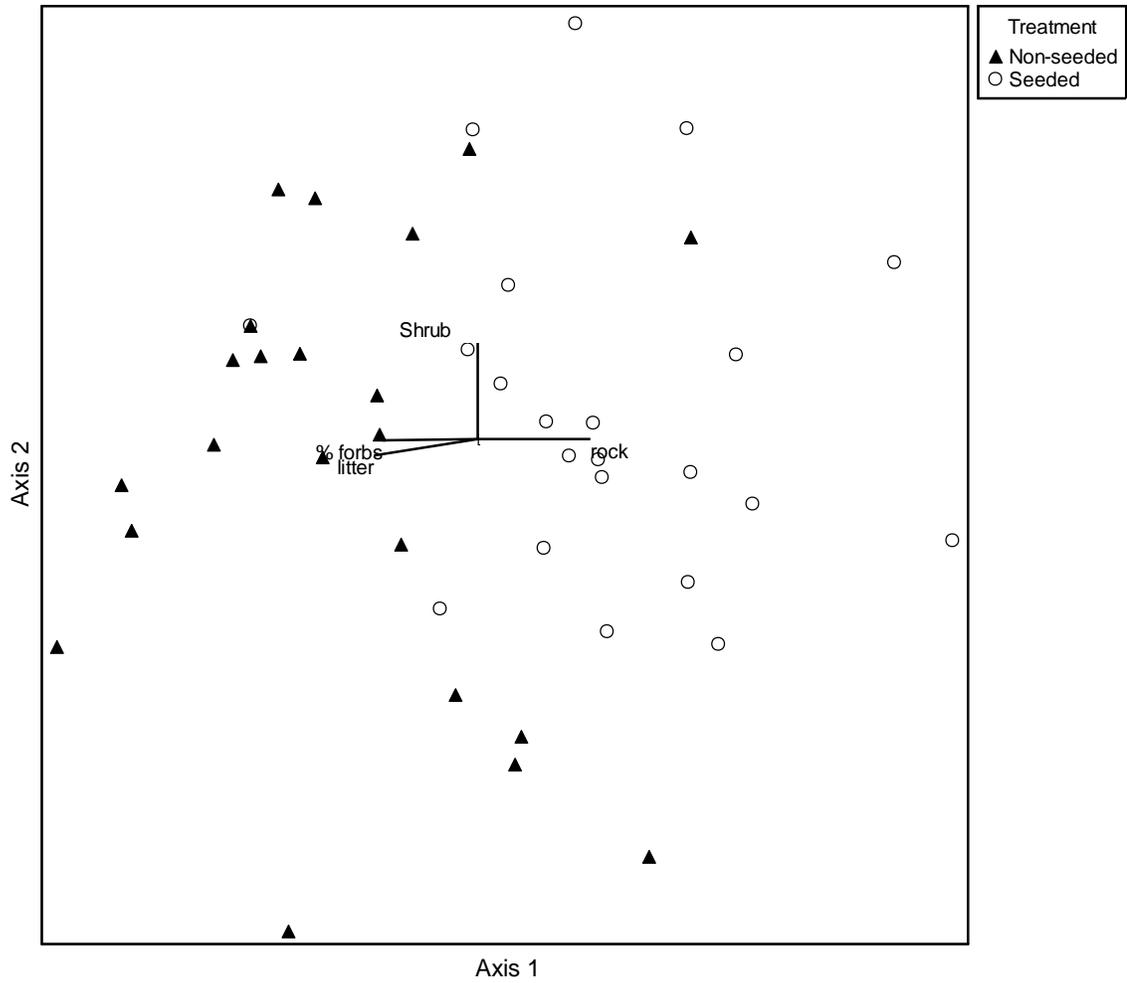


Figure 2.9 Non-metric multidimensional scaling (NMDS) ordination of plant community composition sampled across the Warm Fire ponderosa pine forests in northern Arizona in 2009. The plot was constructed using 109 species found in 44 plots. The final solution had three dimensions. (Stress= 17.46, $p < 0.01$)

CHAPTER THREE

Fire effects on understory plant communities in a ponderosa pine forest

Abstract

Fire was historically one of the most influential disturbances in the ponderosa pine forests of northern Arizona and played a key role in structuring the understory plant communities. We measured the vegetation response to high and low severity fire and compared vegetation cover, species richness and community composition to unburned areas. Total understory vegetation cover was significantly greater in high severity plots (22%) compared to low severity and unburned plots (8%). Species richness was greatest in both low (32) and high severity (33) burned plots compared to unburned (23) plots. Community composition was significantly different in all three treatments. Low severity and unburned plots were more similar in community composition and had similar indicator species whereas high severity plots had a greater variety of species, and were more distinctly different in composition. Graminoids and shrubs had higher cover and were more common in high severity plots. Annual and biennial forbs were present in higher concentration in burned areas and are known to be important components of the post-fire plant community in ponderosa pine forests. Cover of exotic species was greater in burned areas, but average exotic cover was less than 2%. Increased vegetative cover, especially annual and biennial forbs, is often greatest in low severity burns, but in our study, the high severity burns had the greatest cover and richness of this functional group. This study supports the continuation of reintroducing fire to ponderosa pine forests in

northern Arizona as a means to improve forest health and sustainability by altering understory plant communities.

Introduction

Fire was historically a natural and significant disturbance in western forests and particularly in ponderosa pine (*Pinus ponderosa* var. *scopulorum* C. Lawson) ecosystems (Cooper 1960; Agee 1998). Historical fire regimes in the semi-arid ponderosa pine forests consisted of frequent, low intensity, grass-fueled fires every 2-20 years (Swetnam and Baisan 1996; Fulé et al. 1997) that resulted in open forests with groups of pines (Lang and Stewart 1910). With continuous grazing, fire suppression, timber harvest and changing climatic conditions, the forests have been altered and the resulting high levels of fuel loading have produced historically uncommon large and severe crown fires (Covington and Moore 1994; Allen et al. 2002).

Understory herbaceous plant communities in northern Arizona ponderosa pine forests are shaped by the fire regime and the subsequent effects on the forest structure. Species composition of these plant communities invariably change after fire (Crawford et al. 2001; Huisinga et al. 2005; Laughlin et al. 2005; Kuenzi et al. 2008) and while few long-term studies have been done, there are indications that these community changes may still be evident 30 years post-fire (Bataineh et al. 2006). Species richness increases with fire as a result of alterations to the forest canopy and floor (Huisinga et al. 2005; Laughlin et al. 2005; Kuenzi et al. 2008) but is sometimes associated with a subsequent increase in exotic species (Griffis et al. 2000; Crawford et al. 2001; Floyd et al. 2006; Hunter et al. 2006). The change in forest structure promotes herbaceous understory growth and total herbaceous plant cover is higher than in unburned areas (Huisinga et al. 2005; Laughlin et al. 2005; Kuenzi et al. 2008; Sabo et al. 2008). The relationship between changes in species composition, increased exotic presence, and greater richness

and diversity is seen across landscapes adapted to disturbance (Grime 1977; Stohlgren et al. 1999).

The herbaceous diversity of ponderosa pine forests is often maintained by fire and the interactions between both abiotic and biotic components. Abiotic factors such as precipitation, soil properties, elevation and topography play an important role in determining species composition (Laughlin and Abella 2007). Once species begin to colonize or regenerate in the disturbed area, limitations from the abiotic components are compounded with impacts from biotic factors such as tree composition and structure and litter cover (Laughlin and Abella 2007). There has been a decrease in species richness and herbaceous cover in ponderosa pine forests as a result of altered fire regimes. Research in northern Arizona has shown a negative correlation between pine density and understory production (Moore and Deiter 1992; Laughlin et al. 2005; Laughlin and Abella 2007; Sabo et al. 2008). The unnatural accumulation of litter from altered fire regimes also plays a role in defining understory communities. Needle cast inhibits the germination and establishment of some species and can simplify the community and decrease species richness (DiTomaso et al. 1999; Xiong and Nilsson 1999; Laughlin and Abella 2007). Consumption of litter and duff from fire affects annual and biennial forbs most significantly as it prepares a bed of mineral soil with high levels of nutrients and increased soil warmth (Xiong and Nilsson 1999; Laughlin and Abella 2007).

Forested landscapes that have been relatively undisturbed by fire or human impacts typically have low cover of exotics species (Huisinga et al. 2005; Keeley 2006) but when fire is introduced it opens the canopy, exposes bare mineral soil, increases soil pH, and releases phosphorous and nitrogen in available inorganic forms, creating an

improved habitat for exotic germination (Keeley 2006; DiTomaso et al. 2006; Floyd et al. 2006). Exotic species are often quite successful post-disturbance as their seeds are viable for long periods (Grime 1977, Korb et al. 2005). For example, seeds of mullein (*Verbascum thapsus* Bertol.) a common post-fire exotic, can remain viable in the soil for 100 years (Gross and Werner 1978) and can grow 4-7 times faster in exposed soil after a fire (Gross 1980). The increase in available resources subsequently leads to an overall increase in plant diversity and it is suggested that greater biodiversity and more available resources leads to greater exotic invasion (Stohlgren et al. 1999; Floyd et al. 2006).

Plant response to a disturbance such as fire, varies with the species' adaptations and strategies for utilizing resources (Grime 1977). Many common ponderosa pine forest species are well adapted to fire such as: lupine (*Lupinus spp.*) and deervetch (*Lotus spp.*)(nitrogen fixers); ceanothus (*Ceanothus spp.*)(resprouters); squirreltail (*Elymus elymoides* (Raf.) Swezey)and mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc) (bunchgrasses) (DeBano et al. 1998, Huffman and Moore 2004; Laughlin et al. 2006; Kuenzi et al. 2007; Stella 2009). Low severity fires alter the environment in such a way as to give a slight competitive advantage to certain species where high severity fire opens the landscape to species that are well adapted to utilize the influx of favorable conditions (Grime 1977). Ruderal species as described by Grime (1977) are well adapted to systems with consistent and high disturbance and thus there is a suite of species associated with post-fire forests. This suite of species is composed of both natives and exotics and mostly annuals or biennials and is consistent throughout studies in ponderosa pine forests in northern Arizona (Crawford et al. 2001; Bataineh et al. 2006; Kuenzi et al. 2007; Laughlin and Fulé 2008; Stella 2009)

In 2006 the Warm Fire burned across 24,000 ha of the North Kaibab Ranger District on the Kaibab National Forest. It was initially categorized as a Wildland Fire Use fire but due to a dramatic shift in winds and various management decisions, the fire escaped the management boundary and was declared a wildfire. This is a collaborative study which attempts to shed light on the recovery and restoration of the ponderosa pine forest that burned in the Warm Fire. We specifically address the following hypotheses:

1. Fire severity will determine the magnitude of vegetation response with a greater herbaceous cover and species richness in high severity.
2. Burned areas will have a different floristic composition, greater total foliar plant cover and greater plant species richness than unburned areas.
3. Ruderal species will be well represented as indicator species in burned areas.
4. Exotic species foliar cover will be higher in burned areas.
5. Differences in litter cover and overstory tree canopy cover due to fire will be driving factors in vegetation response.

Methods

Study Area

The study sites are located in the Warm Fire on the Kaibab Plateau in the Kaibab National Forest in northern Arizona, USA (Fig. 3.1). Plot locations range in elevation from 2300 to 2590 m and at the landscape-scale have a similar disturbance history in terms of grazing and logging (Trudeau 2006). The fire was ignited by a lightning strike in June, 2006, and consumed a total of 24,000 ha burning across three vegetation

communities: higher elevation mixed conifer consisting of white fir (*Abies concolor* (Gordon and Glendinning) Hoopes), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) and blue spruce (*Picea pungens* Engelm.); mid-elevation ponderosa pine dominated interspersed with quaking aspen (*Populus tremuloides* Michx.), and Gambel oak (*Quercus gambelii* Nutt.) and lower elevation pinyon-juniper woodlands [*Pinus edulis* Engelm., *Juniperus osteosperma* Torr.] (USDA USNF 2007). This study was conducted in ponderosa pine dominated overstory with an understory composed of common grasses, including muttongrass (*Poa fendleriana* (Steud.) Vasey), squirreltail (*Elymus elymoides* (Raf.) Swezey), and Junegrass (*Koeleria macrantha* (Ledeb.) Schult) and common forbs including small leaf pussytoes (*Antennaria parvifolia* Nutt.), Fendler's sandwort (*Arenaria fendleri* A. Gray), and woolly cinquefoil (*Potentilla hippiana* Lehm.).

The 14-year average annual precipitation was 61 cm between 1995 and 2010. Roughly half of the precipitation falls during winter months in the form of snow while the remainder falls during summer rains. Annual precipitation for the years covered by this study was 48 cm in 2007; 33 cm in 2008, 30 cm in 2009 (Fig. 3.2). Precipitation in May and June of 2009 was unusually high whereas precipitation in July and August was lower than average. This may have influenced the number of annual and biennial forbs we recorded as we may have missed some species that bloomed earlier than usual due to the increased early precipitation. Temperatures range from an average January minimum of -5.7 C and an average July maximum of 26.1 C (Western Regional Climate Center, 2009). Soils are derived from Kaibab Limestone parent material (Brewer et al. 1991).

Sampling design

Our study took advantage of a random disturbance (wildfire) and therefore we were unable to employ a more robust sampling design including replication and randomization (van Mantgem et al. 2001). Sample points were randomly selected within fire severity, elevation, vegetation, slope, soils and Burned Area Emergency Response (BAER) treatment strata using ArcView GIS software (ESRI 2006). High and low severity areas were delineated using the Burned Area Emergency Response (BAER) burn severity map derived from Landsat satellite imagery and ground-truthed using the Composite Burn Index (Key and Benson, 2006). Unburned control plots were established within 1 km of the fire perimeter. Site elevation was restricted to within the ponderosa pine vegetation type on slopes less than 28°. Plots were limited to Mollic Eutroboralfs soils (Brewer et al. 1991). Portions of the wildfire section were seeded for restoration under the guidance of the BAER team, but these areas are not included in this study (Chapter 2).

In 2008, two years post-fire, 74 plots were permanently established in unburned controls, low severity burn and high severity burn areas. The 22 plots in high severity areas were the same non-seeded plots used in the study described in Chapter 2. We sampled understory vegetative cover (graminoids, forbs, shrubs and trees), species richness and species composition in 2008 and 2009 during August and early September to capture plants at the greatest production. Understory plant cover hereafter refers to foliar cover of herbaceous plants, shrubs and tree foliage below 1.37 m. Species were classified into four life habits: annual/biennial graminoids (grasses and sedges), perennial graminoids, annual/biennial forbs (ruderal species), perennial forbs, shrubs and

trees. Plots were circular with a 7.32 m radius with six radial transect lines along which nine 1x1 m subplots were placed for understory sampling. Understory plant canopy cover was estimated in each 1x1 m quadrat by species, life form (graminoids, forbs) and total vegetation cover. Species richness was determined for the entire plot. Tree seedling density was recorded in a 3.6 m radius circular sub-plot at the center of the larger plot. Species were classified on the generic or family level when vegetative characteristics were insufficient to identify at the species level. Plant nomenclature and nativity are based on USDA-NRCS (2009) and voucher specimens are located in the Deaver Herbarium in Flagstaff, Arizona.

We measured forest floor cover by visually estimating cover of soil, rock, wood, litter, duff, lichen, moss, and scat at each of the nine subplots. Overstory tree canopy cover was measured with a densitometer in 2009 by counting the number of overstory hits at 33 points along the transect lines. Topographic variables recorded at each site were slope (degrees), aspect, and elevation (m).

Statistical analyses

We analyzed all vegetation data using a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001; McCune and Mefford PC-ORD 5.1), which is a non-parametric test that is useful in analyzing non-normal ecological data in univariate or multivariate datasets. We conducted one-way analyses using Bray-Curtis distance measures for multivariate data and Euclidean distance for univariate data using 9999 permutations, with significance at $\alpha = 0.05$. Differences in species richness were determined by the total number of species per plot per year in each treatment. We tested hypotheses relating to the differences in total herbaceous and woody plant cover and

richness, foliar cover by relevant functional groups and exotic foliar cover. Species that occurred in less than 5% of the plots were omitted from multivariate species composition analysis and ordinations but included in species richness and univariate analysis (McCune and Grace 2002). To specifically test if the unburned, low severity and high severity plots differed from each other in the rate of community change, we used PC-ORD to calculate the Bray-Curtis distance for each plot. This method is similar to calculating the difference between two values in a paired t-test. The dissimilarity was analyzed with a PERMANOVA using Euclidean distance.

Non-metric multidimensional scaling (NMDS) was used to visualize the differences in plant community composition between unburned, low and high severity burned sites. Ordinations were done with PC-ORD V 5.1 (McCune and Mefford 1999) using Bray-Curtis distance measures with 250 runs with real data and 250 runs with randomizations, a maximum of 400 iterations per run and an instability criterion of .00001. Three dimensions were always recommended, however we chose the two axes that represented the most variation to create 2-D representations. We used Pearson's correlation coefficients to determine which species and covariates were most closely associated with the axes of the ordinations.

When differences in plant composition were identified using PERMANOVA, we ran an indicator species analysis (ISA) to determine which species were driving those differences (McCune and Mefford PC-ORD V 5.1). ISA takes into account both relative abundance and relative frequency. Species with an indicator value > 30 and $p < 0.05$ were identified as indicator species (Dufrene and Legendre 1997).

Results

Community response

We recorded a total of 186 vascular plants throughout the area but focused the multivariate analyses on the 93 species that occurred in more than 5% of the plots. In 2008 and 2009, unburned plots had an average of 23 species per plot while low and high severity plots averaged 29 species (Table 3.1). Species richness was significantly higher in both burned plots than unburned plots for both years (Table 3.1). Total foliar cover on unburned and low plots was the same in both years but high severity plots averaged significantly more cover (Table 3.1, Fig. 3.3). Graminoid, forb and shrub cover were significantly greater in high severity plots in 2009, but tree cover was significantly higher in unburned sites in both years and low severity sites in 2009 (Table 3.1; Fig. 3.4). When species were grouped by life history, there were significantly more annuals/biennials and perennials in burned plots in both years (Table 3.1; Fig. 3.5), more legumes in high severity plots in 2009 and tree regeneration did not differ in any severity in either year (Table 3.1).

Floristic composition was significantly different between all three treatments in both years ($p=0.002$ and $p=0.04$, respectively). However, pair-wise comparisons of the community composition showed no difference between unburned and low severity plots in 2008 ($p=0.0658$). Unburned and low severity plots were grouped for ISA analysis in 2008. Four species were indicators for unburned/low severity plots: small leaf pussytoes, Junegrass, ponderosa pine and woolly cinquefoil. Two species were closely associated with low severity plots in 2009 only; Junegrass and beardlip penstemon (*Penstemon barbatus* (Cav.) Roth) (Table 3.2). In 2008 there were 15 indicator species

for high severity and 23 in 2009 (Table 3.2) with some exotic species including: cheatgrass (*Bromus tectorum* L.), prickly lettuce (*Lactuca serriola* L.), Douglas' knotweed (*Polygonum douglasii* Greene), yellow salsify (*Tragopogon dubius* Scop.), dandelion (*Taraxacum officinale* F.H.Wigg) and mullein. Ruderal species that were either annual or biennial forbs, legumes or reproters had a strong showing in high severity: pinyon goosefoot (*Chenopodium atrovirens* Rydb.), Fremont's goosefoot (*Chenopodium fremontii* S. Watson), Wheeler's thistle (*Cirsium wheeleri* (A. Gray) Petr.), horseweed (*Conyza canadensis* (L.) Cronquist), tall annual willowherb (*Epilobium brachycarpum* C. Presl), spreading fleabane (*Erigeron divergens* Torr. and A. Gray), spreading groundsmoke (*Gayophytum diffusum* Torr. and A. Gray), Macoun's cudweed (*Pseudognaphalium macounii* (Greene) Kartesz), silvery lupine (*Lupinus argenteus* Pursh) and aspen (Table 3.2). NMDS ordinations of the plant community show a visual representation of these differences with high severity separating from unburned and low (Fig. 3.6). The rate of species composition change was not significantly different for any treatment between 2008 and 2009 ($p= 0.9408$).

Exotic species

As predicted, burned plots had more exotic cover than unburned (Fig. 3.3); however, both unburned and low severity had < 1% exotic species cover. While high severity plots had significantly more exotics, it was still low cover averaging 1.5% (Table 3.1, Fig. 3.3). Individual high severity plots ranged from 1-5 % exotic cover. There were a total of 21 exotic species found (11% of total) with the most common being cheatgrass, dandelion, yellow salsify and mullein. Musk thistle only occurred on one plot and was observed in one other location. Some of the exotics identified were species that had been

historically seeded, usually as forage for grazing animals including orchardgrass (*Dactylis glomerata* L.), intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth and D.R. Dewey) and timothy grass (*Phleum pratense* L.)

Environmental influences

Our results showed that the cover of substrates (soil, rock and litter) is directly related to burn severity. Litter cover decreased as severity increased while soil and rock cover increased as severity increased (Table 3.1, Fig. 3.7). Cover of litter was significantly lower in burned sites and consequently, soil and rock were significantly higher in burned plots (Table 3.1). Overstory tree canopy cover was also indicative of high severity fire and vegetation response. There was a positive relationship between lower canopy cover in high severity areas and increased herbaceous and shrub response ($p=0.0002$). When overlaying the environmental matrix in the NMDS ordinations, we see litter and canopy cover strongly associated with unburned and low severity sites while rock is strongly associated with high severity sites (Fig. 3.6)

Discussion

Community response

The overall increase in total plant cover in high severity plots and greater species richness in both high and low severity plots supports the theory that fire is one of the essential drivers in the maintenance of understory richness and community structure in ponderosa pine forests. Using remote old-growth ponderosa pine forests in Grand Canyon National Park as reference sites, researchers have concluded that while understory plant communities vary across space and time, there are some common

threads (Laughlin et al. 2004). These forests are characterized by high plant cover, predominately native species, high diversity of species and low fuel loads (Laughlin et al. 2004). Our results are consistent with other studies on fire effects in Arizona forests (Laughlin et al. 2004; Kuenzi et al. 2008) where they found a greater cover and richness response to high severity fire. We also expected the low severity sites to respond to fire with at least a minimal increase in plant cover and richness, but the results varied. Low severity plots were more similar in total plant cover and community composition to unburned plots, but did have significantly greater species richness than unburned plots. One possible explanation for the lack of response of plant cover in low severity is the accumulation of litter precluding the fire from consuming enough to induce a flush of vegetation. Native species are adapted to low severity fire, however, a disturbance with greater magnitude or greater frequency may be necessary to shift the understory composition (Laughlin and Fulé 2008). Since floristic composition was consistently different between unburned and high severity and the rate of compositional change not significantly different, we feel confident that the observed differences are due to fire effects and not inter-annual variability.

The increase in resource availability caused by fire (open canopy, decreased litter cover, flush of nutrients to soil) allowed for annual/biennial and ruderal species to colonize the area. In a post-disturbance seedbank study done by Korb et al. (2005) they reported that the seedbank was predominately composed of annual, ruderal or exotic species. This correlates well with our plant response in high severity. There were 23 species associated with high severity and of those 18 are annuals/biennials, 5 exotics, and 9 ruderals often associated with post-fire environments. Fremont's goosefoot, spreading

fleabane, Wheeler's thistle, horseweed, silvery lupine and Macoun's cudweed have been reported as indicator species for burned areas in several similar studies (Crawford et al. 2001; Huisinga et al. 2005, Laughlin et al. 2005; Kuenzi et al. 2008). Reference sites in ponderosa pine forests on the North Rim of Grand Canyon National Park that have not been subjected to fire suppression indicate that annual and biennial forbs are of great importance to the post-fire plant community (Laughlin et al. 2004). Indicators of low severity were Junegrass and beardlip penstemon. Junegrass is a coarse bunchgrass and when subjected to fire, often survives as the fire burns quickly through the above ground leaf matter, protecting the below-ground biomass (Young 1983). Unburned plots were distinguished by two species intolerant of high-severity fire: small leaf pussytoes and woolly cinquefoil. Small leaf pussytoes is directly killed by fire and a study in lodgepole pine in Yellowstone indicated high abundance only many years after fire (Taylor 1969).

Exotic species.

Our results support the hypothesis that exotic species cover is greater in burned areas. However, total cover of exotic species was less than 2%. A review of exotic presence in ponderosa pine in northern Arizona by McGlone and Egan (2009), found similar results that while the presence of exotic species increased after a fire, the cover of these species was usually less than 10%. In contrast, Crawford et al. (2005) reported a significant presence of exotic species (> 10% cover) in high severity burn areas. However, in our study we used a narrower definition of exotic and considered species like horseweed to be native based on USDA-NRCS PlantsDatabase (2009).

Three exotic species of most concern are cheatgrass, musk thistle and mullein and all three are listed as noxious in at least one southwestern state. Cheatgrass is a well-known invasive that quickly permeates disturbed ecosystems displacing natives and altering fire regimes (Brooks et al. 2004). This species is of great concern in lower elevation forests and deserts, but its ability to persist in ponderosa pine forests and alter the fire regime is unknown (McGlone and Egan 2009). Currently there is no clear method for controlling the invasion of cheatgrass and although there is no evidence supporting a drastic change to ponderosa pine forests, continued monitoring is strongly recommended. We found musk thistle present on one plot and observed a substantial population at one other location in the fire. Forest managers are particularly concerned with the potential spread of musk thistle as it has the ability to rapidly invade and persist, displacing natives and potential forage for wildlife and livestock (USDA USNF 2007; USDA 2010). Mullein is a common post-fire invasive (Crawford et al. 2001; Sabo et al. 2009), and prevalent in the seedbank (Korb et al. 2005) but it is not known to be ecologically significant as it is typically reduced to a minor component of the plant community (Sieg et al. 2003). Prickly lettuce, yellow salsify, and dandelion were all present in high severity plots but were low in cover (<1%). All three species are listed as noxious weeds in at least one state and are well adapted to disturbed areas as they are prolific seed producers with wind-dispersed seeds that can colonize from off-site.

Environmental influences

Plant establishment is often strongly correlated with substrate cover and in ponderosa pine forests, especially soil and litter (DiTomaso et al. 1999; Xiong and Nilsson 1999; Huisinga et al. 2005; Laughlin and Abella 2007). Our study showed that

as litter cover increased, total vegetative cover decreased and conversely, when soil cover increased, so did vegetative cover. On low severity sites litter cover was still 53% two years post-fire while high severity sites had only 32% cover. Decreasing unnaturally high levels of litter through fire creates an opportunity for understory growth. While we did not measure litter and duff depth in this study, Huisinga et al. (2005) did so in a high severity burn in a mixed conifer forest on the Kaibab Plateau and found it significantly reduced in the burned areas. The depth and cover of litter and duff determines the likelihood of seed germination (Sydes and Grime 1981) and particularly with annual species (Laughlin et al. 2005). We also observed that overstory tree canopy cover was significantly lower when understory herbaceous and shrub cover was high. This inverse relationship of high species richness, greater annual/biennial and graminoid cover compared to less canopy cover is likely due to the increased light and nutrient availability (Moore and Deiter, 1992; Sabo et al. 2009).

Management implications and recommendations

One major goal of the Wildland Fire Use program is to begin the process of reintroducing fire into ecosystems where historically it was prevalent and currently is lacking (USDA USNF 2007). With the Warm Fire, managers hoped to: decrease surface fuels; open the forest canopy to allow for the regeneration of pine trees and restoration of understory vegetation; reduce the threat of landscape-scale high severity fire; and return fire as an ecological process to the landscape (USDA USNF 2007). The WFU portion of this fire should be viewed as a success in that it achieved most of the desired goals and moved closer to restoring the landscape. However, it will be necessary to continue implementing fire across the landscape to continue the transition to an ecosystem with

frequent fires; one low severity fire after 100 years of suppression might not be enough of a disturbance. The increase in exotic plant cover as a result of high severity fire warrants continued monitoring. Restoration projects such as landscape-scale thinning and targeted exotic removal (Hunter and Omi 2006) may help to mitigate the increase in exotic species in the future (Allen et al. 2002).

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Tables and figures

Table 3.1 Actual data values for all treatments in both years. Numbers represent foliar cover of herbaceous species, shrubs and trees unless otherwise noted. Species richness is the average number of species/plot in the treatment. Letters indicate a significant difference ($p < 0.05$) among treatments in 2008 and 2009.

Category	2008			2009		
	U	L	H	U	L	H
Vegetative cover (%)						
Total foliar cover	7.535 a	8.627 a	21.68 b	8.021 a	8.924 a	23.26 b
Exotic	0.085	0.084	1.542	0.063 a	0.027 b	1.615 c
Native	7.449	8.391	20.10	7.956 a	8.626 a	21.59 b
Functional groups (%)						
Graminoids	1.883	2.168	2.435	1.927 a	2.515 a	4.370 b
Forbs	3.588 a	4.391 a	16.02 b	3.275 a	4.139 a	14.21 b
Shrubs	1.472 ab	0.896 a	2.981 b	1.917	1.053	4.362
Trees	0.589 ab	1.171 a	0.179 b	0.902a	1.194 ab	0.250 b
Annual/Biennial	0.469 a	0.600 a	6.354 b	0.194 a	0.436 a	4.206 b
Perennial	7.063	8.027	15.27	7.825 a	8.469 a	18.99 b
Legumes	1.125	1.389	3.423	1.074 a	1.265 ab	4.538 b
Community composition						
Richness	22 a	29 b	26 ab	25 a	30 b	32 b
Abiotic variables (%)						
Litter	73.71 a	53.61 b	32.95 c	79.52 a	69.20 b	45.96 c
Soil	3.731 a	11.27 b	20.36 c	1.614 a	6.494 b	9.045 b
Rock	3.114 a	8.987 b	16.45 c	2.551 a	7.020 b	12.823 b

Table 3.2. Indicator species for 2008 and 2009. Unburned and low plots were analyzed together in 2008. Only species which were significant indicators (IV > 30, p < 0.05) are listed in this table.

Severity	Species	IV 2008	Severity	IV 2009	Life History	Life Form
Unburned and Low	<i>Antennaria parvifolia</i>	70.4	Un- burned	-	P	F
	<i>Pinus ponderosa</i>	82.0		56.4	P	T
	<i>Potentilla hippiana</i>	39.2		54.6	P	F
	<i>Koeleria macrantha</i>	43.3	Low	44.3	P	G
	<i>Penstemon barbatus</i>	-		48.6	P	F
High	<i>Agoseris glauca</i>	-	High	33.9	B	F
	<i>Androsace septentrionalis</i>	30.1		-	A	F
	<i>Arenaria lanuginosa ssp. saxosa</i>	-		44.9	P	F
	<i>Bromus tectorum*</i>	40.4		59.2	A	G
	<i>Chenopodium atrovirens</i>	-		36.4	A	F
	<i>Chenopodium fremontii</i>	85.0		72.3	A	F
	<i>Cirsium wheeleri</i>	70.0		65.6	A/B	F
	<i>Conyza canadensis</i>	45.5		45.4	A	F
	<i>Epilobium brachycarpum</i>	-		50.2	A	F
	<i>Erigeron divergens</i>	79.7		69.9	B	F
	<i>Erigeron flagelleris</i>	-		44.4	P	F
	<i>Eriogonum racemosum</i>	72.3		47.1	P	F
	<i>Gayophytum diffusum</i>	74.3		71.4	A	F
	<i>Heliomeris multiflora</i>	-		35.9	B	F
	<i>Lactuca serriola*</i>	59.0		81.0	A	F
	<i>Lupinus argenteus</i>	53.5		45.2	P	F
	<i>Packera multilobata</i>	-		63.1	B	F
	<i>Polygonum douglasii</i>	56.8		64.2	A	F
	<i>Poa fendleriana</i>	-		48.8	P	G
	<i>Pseudognaphalium macounii</i>	65.2		67.1	A/B	F
<i>Taraxacum officinale*</i>	71.0	71.3	A	F		
<i>Tragopogon dubius*</i>	-	40.6	B	F		
<i>Verbascum thapsus*</i>	36.4	40.9	B	F		

* = exotic; P= Perennial, A= Annual, B= Biennial, G= Grass, F= Forb, S= Shrub, T= Tree.

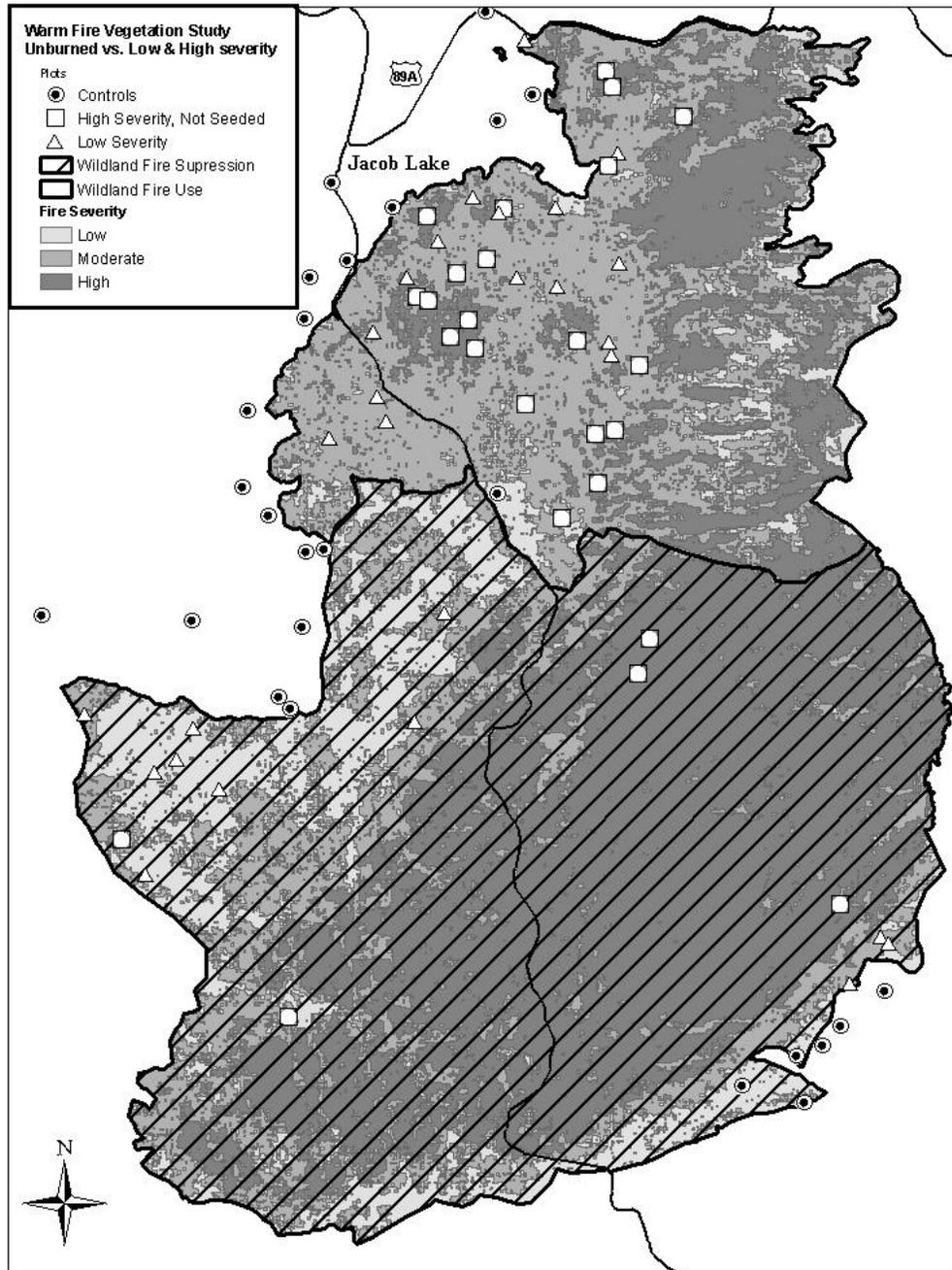


Figure 3.1. Location of study site. Perimeter of the Warm Fire; the northern portion of the fire (no crosshatch) was managed as a WFU while the southern portion (crosshatched) was managed as a wildfire and was subjected to post-fire mitigation. The fire encompassed 24,000 ha across three vegetation types. Burn severity is indicated by varying shades of grey. Seeded plots are indicated by circles and non-seeded plots by squares.

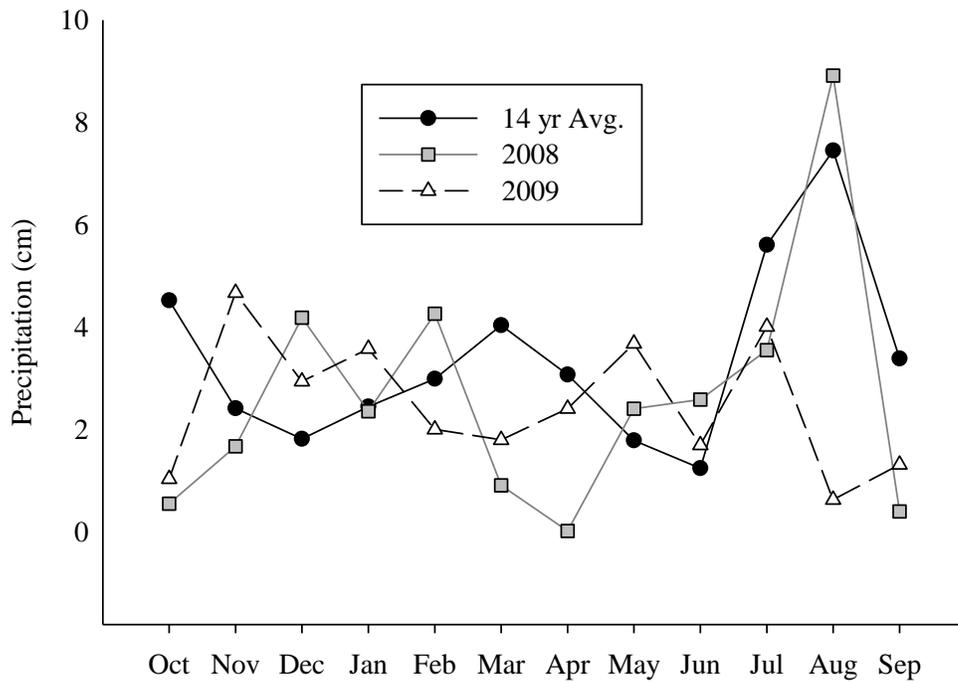


Figure 3.2. 14-year average and monthly precipitation for sites during sampling years. Precipitation data was collected at the Warm Springs Canyon weather station (36° 42' 00" 112° 13' 48") at 2441 m elevation.

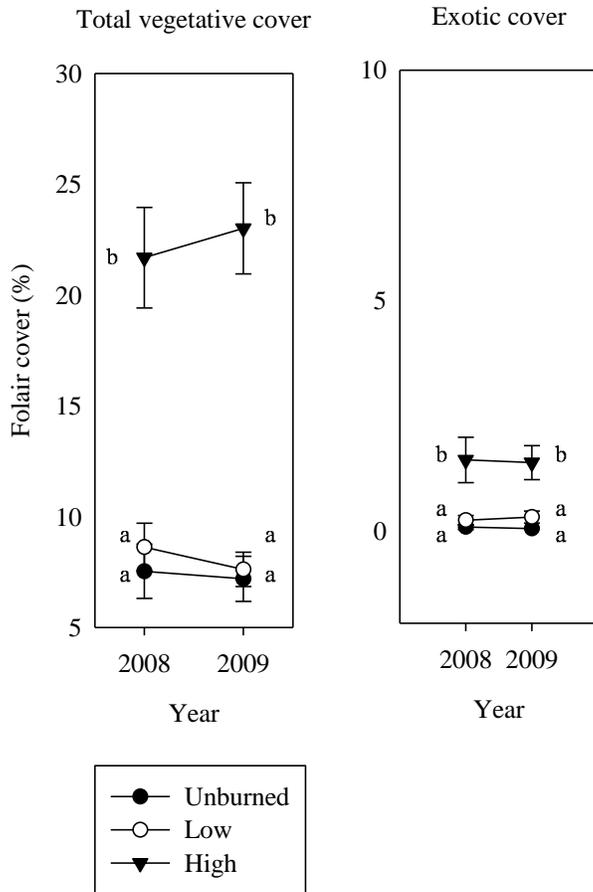


Figure 3.3. Average total cover (foliar for herbaceous, shrub and tree species less than 1.37 m tall and basal cover for tree species greater than 1.37 m tall) and exotic cover (%) by fire severity. Significant differences in total cover are indicated with different letters shown above average cover. Vertical bars represent +/- 1 standard error.

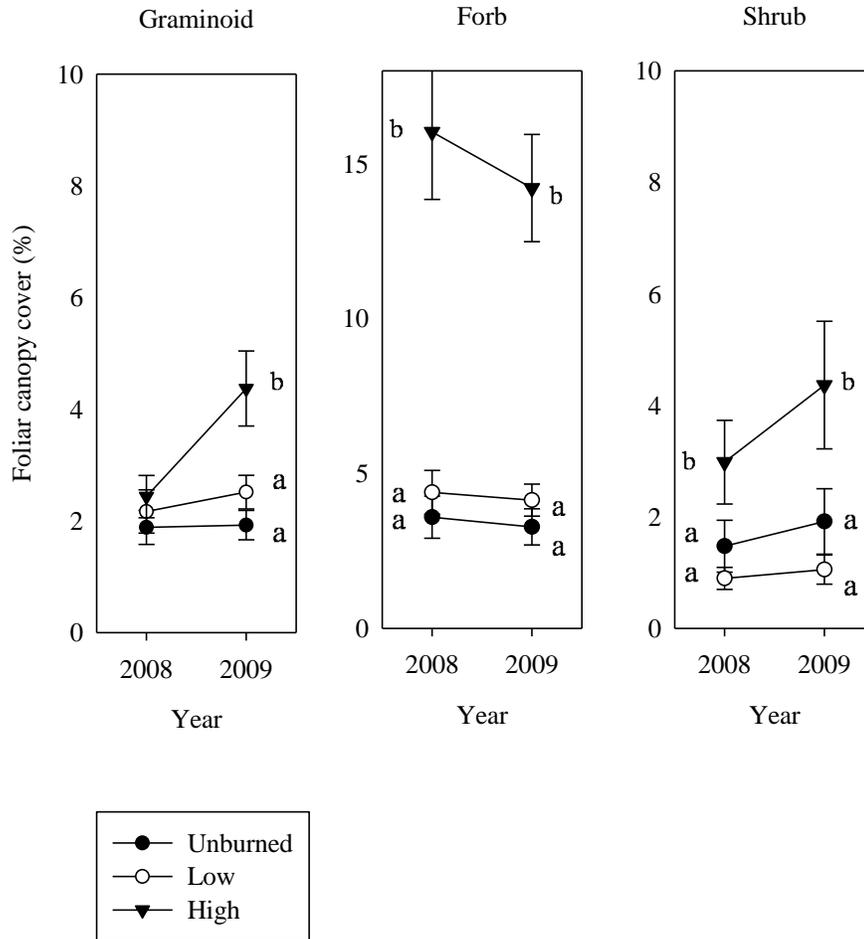


Figure 3.4. Average foliar cover (%) of graminoids, forbs and shrubs by fire severity and year. Significant differences in average cover are indicated with different letters shown above cover. Vertical bars represent +/- 1 standard error.

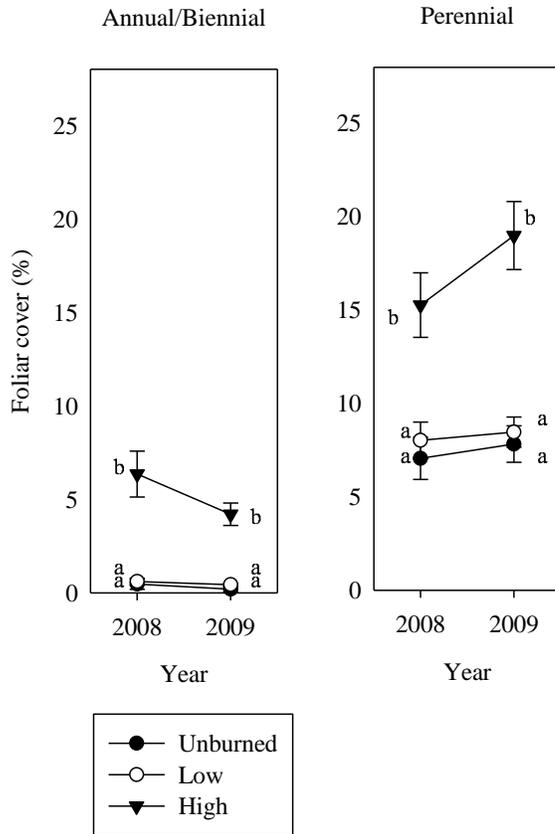


Figure 3.5. Average foliar cover by life form (annual/biennial and perennial), fire severity and year. Significant differences in average cover are indicated with different letters shown above cover. Vertical bars represent +/- 1 standard error.

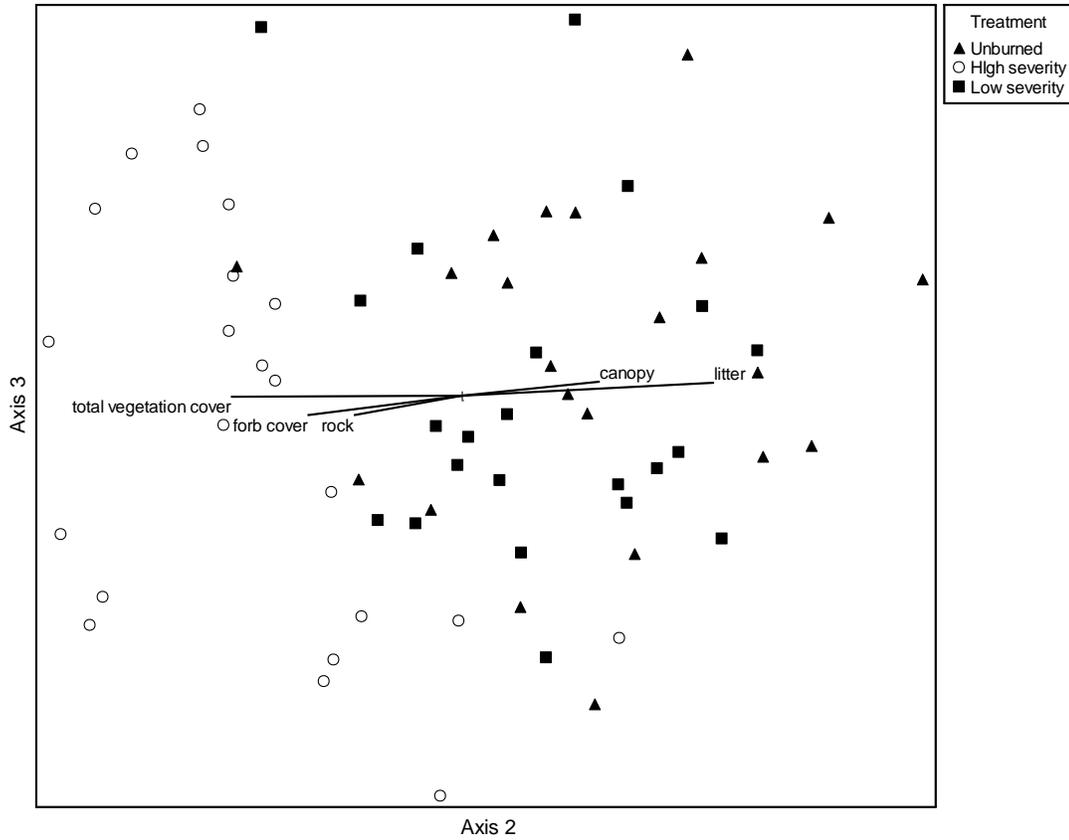


Figure 3.6. Non-metric multidimensional scaling (NMDS) ordination of plant community composition sampled across the Warm Fire ponderosa pine forests in northern Arizona in 2009. The plot was constructed using 88 species found in 66 plots. The final solution had three dimensions. (Stress= 17.69103, $p < 0.01$, 177 iterations).

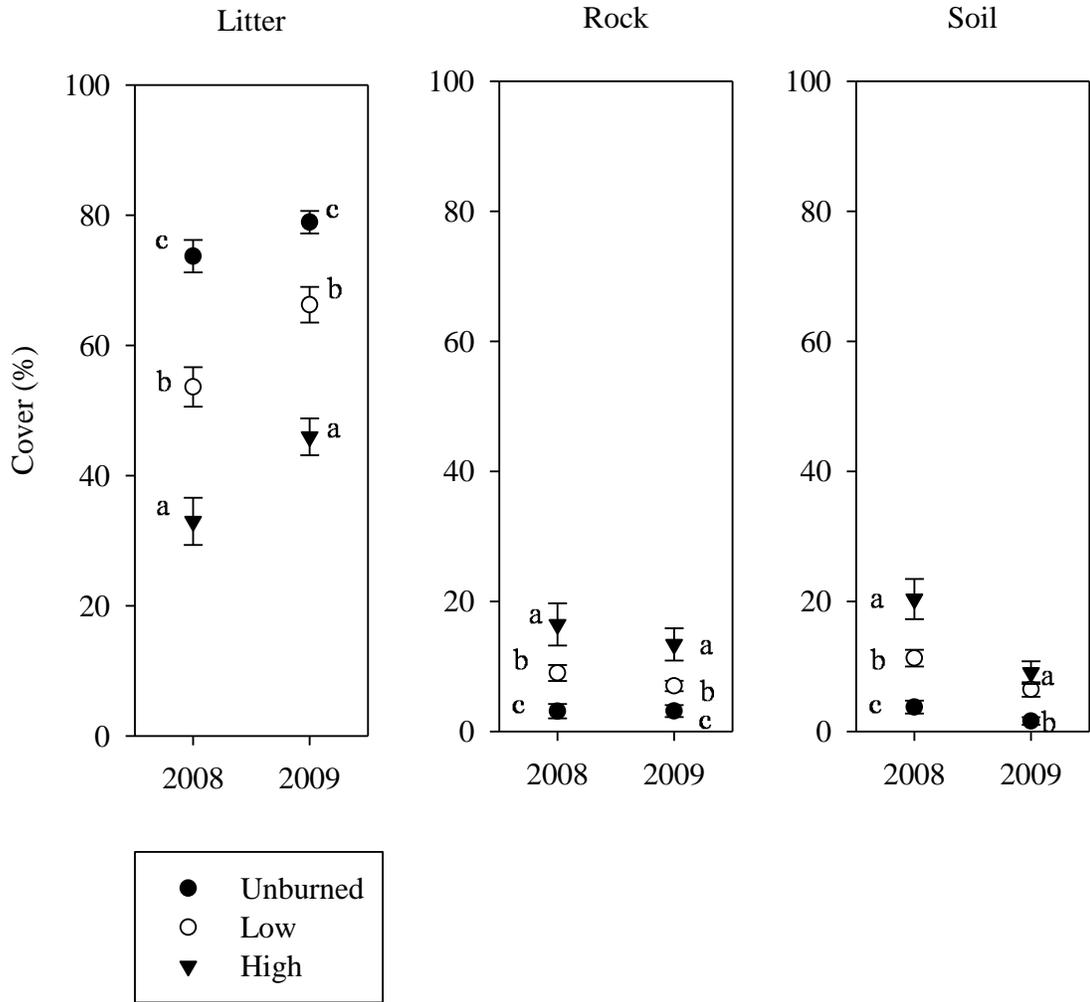


Figure 3.7. Average cover of litter, rock and soil (%) by year and fire severity. Significant differences in average cover are indicated with different letters shown above cover. Vertical bars represent +/- 1 standard error

CHAPTER 4

Conclusions

Northern Arizona contains the largest contiguous area of ponderosa pine forests in the world but, after a century of unsustainable land management and climatic fluctuations, the historic forest structure is rare across the landscape. These forests are degraded and unhealthy with nearly 10 times higher tree densities which leave the forests more susceptible to disease and catastrophic wildfires which threaten communities, wildlife and watersheds (Allen et al. 2002). Landscape scale treatments are needed to improve forest conditions. Through the restoration of natural ecological processes (i.e., low severity fire) and implementation of thinning treatments, forest managers can decrease the risk of high severity crown fires (Agee 1993; Allen et al. 2002). Multi-agency, collaborative and community based projects like the Statewide Strategy for Restoring Arizona's Forests are working to instigate landscape-scale restoration projects to preserve the biodiversity in northern Arizona ponderosa pine forests. Managers and stakeholders are working towards a plan to safely reintroduce fire on a landscape scale through thinning projects proposed on over 1 million acres of forest (GFHC 2009). Fires will forever be a significant disturbance in these forests but can be integrated more safely and maintain ecological integrity when done with scientifically based protocols and forward-thinking (Allen et al. 2002).

Current post-fire mitigation often contradicts the ultimate goals of creating and maintaining ecologically stable and diverse ecosystems (Beschta et al. 2003). Federal land managers are required by law to conduct post-fire evaluations for the risk of

watershed damage and spread of exotics (Robichaud et al. 2000). If there is a substantial threat, the BAER teams are responsible for activating treatments (Robichaud et al. 2000). The three most common treatments are seeding, contour felling of logs and mulching. Contour felling has had some success for controlling hill slope erosion but there have been very few studies and it is expensive to install and monitor (Wagenbrenner et al. 2006). Applying mulch to a slope to control erosion is often effective at decreasing erosion but is very expensive and there are concerns regarding the accidental introductions of non-native species (Robichaud et al. 2000, Kruse et al. 2004). Grass seeding is the most common and most studied form of post-fire treatment and results show that it is generally ineffective at decreasing soil erosion (Robichaud et al. 2000, Peppin et al. in review).

Total vegetation cover is used to determine the success of seeding (Beyers 2004). A recent review of published seeding studies by Peppin et al. in review concludes that while seeding is a common choice, it is not effective at producing the required 60% ground cover to reduce erosion. The results of this study support this review in that the seeded species averaged only 6% cover one-year post-fire and seed was most prevalent on gradual slopes. Seeded sites actually had less total cover than non-seeded sites in the Warm Fire. Annual species are often chosen as they will exit the system within 2-3 years of seeding but in this study the ryegrass is still present. The long-term persistence of this intentionally introduced species is currently unknown and managers and stakeholders will need to continue monitoring.

One of the biggest concerns in the post-fire environment is the establishment and spread of exotic species across the disturbed landscape. A primary goal of seeding in

high severity areas is to mitigate this effect (USDA 2004). Overall, I observed greater frequency and abundance of exotics as fire severity increased (unburned, low severity and high severity) and found less exotic cover in seeded versus non-seeded sites. More exotics were also closely associated with both non-seeded and high severity burned sites. However, the total cover of exotics was less than 2% for all treatments and severities and the difference in cover between seeded and non-seeded sites was 1%. Thus the impacts of seeding appear to be relatively marginal. There was no significant difference in exotic cover when *Lolium perenne* spp. *multiflorum* [(Lam.) Husnot)] was included in the analysis. While the goal of seeding is to decrease exotics, treatments are at the same time introducing an exotic and it could arguably be included in the analysis.

Exotic species response to fire is variable depending on land history, reproductive strategies and life history traits. We observed one particularly insidious exotic *Carduus nutans* (L.) on one non-seeded site but this species is restricted to a few specific and isolated locations and is being monitored and controlled by the Kaibab National Forest. *Bromus tectorum* (L.) followed the same line as most exotics and was present more often in burned areas and non-seeded sites. However, the difference between seeded and non-seeded plots was < 0.05% cover and declined in non-seeded sites but increased in seeded sites from 2008 to 2009. Several exotic grass species that were present throughout the sites are relics of previous seeding efforts to increase forage after logging projects and include *Thinopyrum intermedium* [(Host) Barkworth and D.R. Dewey], *Dactylis glomerata* (L.), and *Phleum pratense* (L.). These species have been present in the system for years and are at this point naturalized into the ecosystem (Trudeau 2007). *Verbascum thapsus* (Bertol.) was particularly ubiquitous at a few non-seeded sites. Because their

seeds are able to survive for centuries in the soil (Korb et al. 2004), it is likely to remain in the system regardless of post-fire mitigation. *Taraxacum officinale* (L.) will likely remain in the community as well, but so far it has not had any dramatic effects on the ecosystem.

Fire is known to stimulate the growth and diversity of the understory plant community. I saw an increase in vegetation cover and species richness with increased fire severity. The plant community composition was significantly different from low severity and unburned sites as well as between seeded and non-seeded sites. I expected to see the community differences between fire severities, but the differences associated with seeding are more significant and troubling. Although ryegrass cover was relatively low, there is evidence that it competes for space and may displace natives thus altering the initial community composition and possibly the community trajectory. My study adds to that growing body of evidence (Barclay et al. 2004; Peppin et al. in review). Long term monitoring is needed to determine the ultimate effects on the community.

My results suggest that understory vegetation will persist and flourish even after a high severity fire. Maintenance and rehabilitation of threatened watersheds is an important component of post-fire treatments, but seeding with a non-native grass has not shown to provide adequate cover to control erosion and contradicts management goals of ecological resiliency (Peterson et al. 1998; Peppin et al. in review). Even with fires outside the natural range of variability, ponderosa pine ecosystem processes will encourage the regeneration of plant communities.

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