

PRE-FIRE TREATMENTS HAVE PERSISTENT EFFECTS ON POST-FIRE PLANT COMMUNITIES

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ABSTRACT

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Wildfires characterized by large areas of high severity are increasingly occurring in ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests of the Southwest to extents that are out of the natural range of variability. Managers are now routinely applying thinning and/or burning treatments to reduce fire severity. To investigate the effects of pre-fire treatments and fire severity on post-fire vegetation recovery, we re-measured established plots on the 2002 Rodeo-Chediski Fire on the White Mountain Apache Tribal (WMAT) lands eight years post-fire and the Apache-Sitgreaves National Forest (ASNF) nine years post-fire.

On the WMAT lands we re-measured 70 plots stratified by fire severity (high, low) and pre-fire treatment (untreated, and cut/burned). We found significantly higher overall plant cover, exotic forb cover (although this was still low, <1%) and pine regeneration frequency in high severity areas, and highly significant overall differences in plant community composition and abundance between severity classes. Pre-fire treatment also influenced vegetation response within fire severity class. In particular, pine regeneration was more frequent in pre-fire treated areas than untreated areas for both severity classes, which we linked to a generally more open canopy in treated low severity fire areas and to a more heterogeneous neighborhood severity pattern in treated high severity areas.

On the ASNF portion of the study, we re-measured 80 plots in paired pre-fire thinned sites, which were less severely burned, and pre-fire unthinned sites that were more severely burned. Plant community composition and abundance in thinned and unthinned areas were

converging nine years post-fire; however, persistent differences included significantly higher overall plant cover, as well as higher mean shrub cover in the untreated areas.

A low exotic species response was observed on both study areas, but we did detect an increased frequency of some exotic species compared to the initial observations. Studies throughout the Southwest have documented varying rates of exotic species invasions, suggesting there is no clear pattern between fire severity and exotic species response. Although high severity fire can increase growing space for exotic species, post-fire management practices, on-site propagules and weather patterns may be the more important drivers of exotic response.

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PREFACE

This thesis contains two manuscripts intended for publication, and these chapters both use “we” instead of “I” because they will include co-authors. These manuscripts are Chapter 2: “The influence of pre-fire treatment on post-fire plant community dynamics through time” and Chapter 3: “Pre-fire management treatments have lasting effects on post-fire plant community response.” The literature cited in each chapter is listed at the end of that chapter.

CHAPTER 1

Introduction

In much of the western United States, global climate change has been linked to increased fire severity (Miller *et al.*, 2009), frequency and extent (Westerling *et al.*, 2006; Littell *et al.*, 2009). This trend is expected to continue in the Southwest, where a warmer and drier climate is predicted (Seager *et al.*, 2007). Southwestern ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests are at particularly high risk, since these forests are now characterized by high densities of small trees with closed canopies (Cooper 1960, Covington and Moore 1994). Large scale, stand-replacing fires are of concern because they are out of the range of natural variability for these ecosystems (Fulé *et al.* 2003), which means that the post-fire landscapes are necessarily recovering under novel conditions, and their future trajectories are not easily predicted.

Rather than regenerate as forest, these areas have the potential to persist as vegetation type conversions to shrublands or grasslands (Savage and Mast, 2005), for several reasons. First, pine recruitment may decline under warming climate, since successful seedling establishment is sensitive to moisture and temperature (Puhlick *et al.*, 2012). Second, high severity fire may promote species that have the ability to resprout post-fire. Early site capture by sprouting species may limit the establishment of seeder species such as ponderosa pine through competition for resources (Fulé and Covington, 1998; Barton, 2002). In addition, these novel post-fire communities may be more susceptible to frequent high severity fire, which could limit tree recruitment and create positive feedbacks between climate, vegetation and fire (Fried *et al.*, 2004). Even where forest structure eventually does re-establish, it is likely to take decades (Haire and McGarigal, 2008, 2010), and the plant communities in severely burned areas are

likely to remain distinct from those in forested areas for many years (Bataineh *et al.*, 2006). Such changes to native vegetation could have significant ramifications for many trophic levels, including herbivores, pollinators, as well as native wildlife communities (Beier *et al.*, 2008).

High severity fire may also promote exotic species invasions, which are of concern because they can negatively impact native plant communities (Levine *et al.*, 2003) and alter future fire regimes (Brooks *et al.*, 2004). These high severity disturbances are extensive enough to open up growing space for early seral colonizers that are generally ruderal, annual/biennial, shade-intolerant species (Egler, 1954; Grime, 1977; Keeley *et al.*, 1981). Although exotic species exhibit a myriad of plant strategies and tolerances, many of them are well-suited to fill this role (Sutherland, 2004; Martin *et al.*, 2009). In addition, the degree to which invasions occur is not limited to disturbance severity; weather patterns and propagule pressure are also important factors (Lockwood *et al.*, 2005; McGlone *et al.*, 2009). In the Southwest, several studies have linked high severity fire with exotic species invasions in semi-arid ecosystems (Crawford *et al.*, 2001; Floyd *et al.*, 2006; Dodge *et al.*, 2008; Rew and Johnson, 2010). However, other studies have documented minor responses by exotic species (Huisinga *et al.*, 2005; Kuenzi *et al.*, 2008; McMaster, 2010), thus limiting our ability to predict exotic species invasions in relation to fire.

In response to the threat of high severity fire and these undesirable consequences, managers are increasingly applying fuels treatments, such as thinning and burning, in ponderosa pine forests. These treatments generally reduce fire severity where applied (Pollet and Omi, 2002; Finney *et al.*, 2005; Fulé *et al.*, 2012). Unfortunately, the disturbance caused by the fuels reduction treatments can also lead to exotic species invasions (Keeley, 2006; McGlone *et al.*, 2009; Sabo *et al.*, 2009).

The 2002 Rodeo-Chediski Fire of east-central Arizona burned approximately 189,000 hectares in ponderosa pine forests and pinyon-juniper (*Pinus edulis* Engelm.–*Juniperus*

depeana Steud.) woodlands. At the time, this fire was the largest fire on record in the Southwest by an order of magnitude, and much of it burned severely. Since the fire burned over areas where landscape-scale fuels treatments were conducted, it offered an exceptional opportunity to examine the effects of fire severity and pre-fire treatment on vegetation response. We re-measured existing plots in the Rodeo-Chediski Fire in order to examine longer-term trends, specifically focusing on patterns of exotic species invasions and pine regeneration. The plots were originally established in 2004, when both overstory, understory and fuels characteristics were measured, and re-visited in 2005, when the understory characteristics were measured again (Strom, 2005; Kuenzi, 2006; Strom and Fulé, 2007; Kuenzi *et al.*, 2008).

Chapter 2 presents data from the Apache-Sitgreaves National Forest portion of the fire, where we re-measured paired pre-fire thinned and unthinned sites in 2011. In order to assess how pre-fire treatment, and the resultant severity, influenced plant communities through time we conducted a repeated measures analysis on the three years for which we have data (2004, 2005, 2011). Chapter 3 presents data from the White Mountain Apache Tribal land, where we re-measured plots stratified by fire severity (low and high) and pre-fire treatment (untreated, or cut and burned). This allowed us to more discretely quantify vegetation response in relation to severity. It also enabled us to examine how treatment influenced the vegetation response within both low and high severity burned areas. Finally, Chapter 4 offers management recommendations based on our findings. We hope our analyses of these longer-term datasets help managers to better understand how pre-fire treatments may influence post-fire plant communities and future forest regeneration.

REFERENCES

- Barton, A.M., 2002. Intense wildfire in southeastern Arizona: transformation of a Madrean oak-pine forest to oak woodland. *Forest Ecology and Management* 165, 205-212.
- Bataineh, A.L., Oswald, B.P., Bataineh, M.M., Williams, H.M., Coble, D.W., 2006. Changes in understory vegetation of a ponderosa pine forest in northern Arizona 30 years after a wildfire. *Forest Ecology and Management* 235, 283-294.
- Beier, P., Rogan, E.C., Ingraldi, M.F., Rosenstock, S.S., 2008. Does forest structure affect reproduction of northern goshawks in ponderosa pine forests? *Journal of Applied Ecology* 45, 342-350.
- Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677-688.
- Crawford, J.S., Wahren, C.H.A., Kyle, S., Moir, W.H., 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *Journal of Vegetation Science* 12, 261-268.
- Cooper, C.F., 1960. Changes in vegetation, structure, and growth of south-western pine forests since white settlement. *Ecological Monographs* 30, 130-164.
- Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa forest structure - changes since Euro-American settlement. *Journal of Forestry* 92, 39-47.
- Dodge, R.S., Fulé, P.Z., Sieg, C.H., 2008. Dalmatian toadflax (*Linaria dalmatica*) response to wildfire in a southwestern USA forest. *Ecoscience* 15, 213-222.
- Egler, R.E., 1954. Vegetation science concepts I. Initial floristic composition: A factor in old-field vegetation development. *Vegetatio* 4, 412-417.
- Finney, M.A., McHugh, C.W., Grenfell, I.C., 2005. Stand- and landscape-level effects of prescribed burning on two Arizona wildfires. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 35, 1714-1722.
- Floyd, M.L., Hanna, D., Romme, W.H., Crews, T.E., 2006. Predicting and mitigating weed invasions to restore natural post-fire succession in Mesa Verde National Park, Colorado, USA. *International Journal of Wildland Fire* 15, 247-259.
- Fried, J.S., Torn, M.S., Mills, E., 2004. The impact of climate change on wildfire severity: A regional forecast for northern California. *Climatic Change* 64, 169-191.
- Fulé, P.Z., Covington, W.W., 1998. Spatial patterns of Mexican pine-oak forests under different recent fire regimes. *Plant Ecol.* 134, 197-209.

- Fulé, P.Z., Heinlein, T.A., Covington, W.W., Moore, M.M., 2003. Assessing fire regimes on Grand Canyon landscapes with fire-scar and fire-record data. *International Journal of Wildland Fire* 12, 129-145.
- Fulé, P.Z., Crouse, J.E., Roccaforte, J.P., Kalies, E.L., 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *Forest Ecology and Management* 269, 68-81.
- Grime, J.P., 1977. Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111, 1169-1194.
- Haire, S.L., McGarigal, K., 2008. Inhabitants of landscape scars: Succession of woody plants after large, severe forest fires in Arizona and New Mexico. *Southwestern Naturalist* 53, 146-161.
- Haire, S.L., McGarigal, K., 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. *Landscape Ecology* 25, 1055-1069.
- Huisinga, K.D., Laughlin, D.C., Fulé, P.Z., Springer, J.D., McGlone, C.M., 2005. Effects of an intense prescribed fire on understory vegetation in a mixed conifer forest. *Journal of the Torrey Botanical Society* 132, 590-601.
- Keeley, J.E., 2006. Fire management impacts on invasive plants in the western United States. *Conservation Biology* 20, 375-384.
- Keeley, S.C., Keeley, J.E., Hutchinson, S.M., Johnson, A.W., 1981. Postfire succession of the herbaceous flora in southern-California chaparral. *Ecology* 62, 1608-1621.
- Kuenzi, A.M., 2006. Pre-fire treatment effects and understory plant community response on the Rodeo-Chediski fire, Arizona. M.S. Thesis, School of Forestry, Flagstaff, AZ, Northern Arizona University.
- Kuenzi, A.M., Fulé, P.Z., Sieg, C.H., 2008. Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. *Forest Ecology and Management* 255, 855-865.
- Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., Lavorel, S., 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270, 775-781.
- Littell, J.S., McKenzie, D., Peterson, D.L., Westerling, A.L., 2009. Climate and wildfire area burned in western U. S. ecoprovinces, 1916-2003. *Ecological Applications* 19, 1003-1021.
- Lockwood, J.L., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution* 20, 223-228.
- Martin, P.H., Canham, C.D., Marks, P.L., 2009. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology and the Environment* 7, 142-149.

McGlone, C.M., Springer, J.D., Laughlin, D.C., 2009. Can pine forest restoration promote a diverse and abundant understory and simultaneously resist nonnative invasion? *Forest Ecology and Management* 258, 2638-2646.

McMaster, M.A., 2010. Effects of fire and post-fire seeding on plant communities in a ponderosa pine forest. M.S. Thesis, School of Forestry, Flagstaff, AZ, Northern Arizona University.

Miller, J.D., Safford, H.D., Crimmins, M., Thode, A.E., 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12, 16-32.

Pollet, J., Omi, P.N., 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *International Journal of Wildland Fire* 11, 1-10.

Puhlick, J.J., Laughlin, D.C., Moore, M.M., 2012. Factors influencing ponderosa pine regeneration in the southwestern USA. *Forest Ecology and Management* 264, 10-19.

Rew, L.J., Johnson, M.P., 2010. Reviewing the Role of Wildfire on the Occurrence and Spread of Invasive Plant Species in Wildland Areas of the Intermountain Western United States. *Invasive Plant Science and Management* 3, 347-364.

Sabo, K.E., Sieg, C.H., Hart, S.C., Bailey, J.D., 2009. The role of disturbance severity and canopy closure on standing crop of understory plant species in ponderosa pine stands in northern Arizona, USA. *Forest Ecology and Management* 257, 1656-1662.

Savage, M., Mast, J.N., 2005. How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 35, 967-977.

Seager, R., Ting, M.F., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.P., Harnik, N., Leetmaa, A., Lau, N.C., Li, C.H., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316, 1181-1184.

Strom, B.A., 2005. Pre-fire treatment effects and post-fire forest dynamics on the Rodeo-Chediski burn area, Arizona. M.S. Thesis, School of Forestry, Flagstaff, AZ, Northern Arizona University.

Strom, B.A., Fulé, P.Z., 2007. Pre-wildfire fuel treatments affect long-term ponderosa pine forest dynamics. *International Journal of Wildland Fire* 16, 128-138.

Sutherland, S., 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. *Oecologia* 141, 24-39.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940-943.

CHAPTER 2

The influence of pre-fire fuel reduction treatments on post-wildfire plant community dynamics
through time

ABSTRACT

We used a multi-year dataset from the 2002 Rodeo-Chediski Fire to detect post-fire trends in plant community response in burned ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests of east-central Arizona. Within the burn perimeter, we examined the effects of pre-fire fuels treatments on post-fire vegetation recovery by comparing paired thinned and unthinned sites on the Apache-Sitgreaves National Forest. We sampled these paired sites in 2004, 2005 and 2011. There were significant differences in plant community composition by species cover data in 2004 and 2005, but community composition in treated and untreated plots was beginning to converge in 2011. Total plant cover was significantly higher in untreated areas for all three years. Plant cover generally increased between 2004 and 2005 and markedly decreased in 2011, with the exception of shrubs which steadily increased through time. The sharp decrease in forb and graminoid cover in 2011 is likely due in part to the well below-average precipitation in the previous year. Annual/biennial forb and graminoid cover decreased relative to perennial cover through time, consistent with the patterns predicted by the initial floristics hypothesis. In contrast to our expectations, exotic plant response on these sites was highly variable and not limited to the immediate post-fire, annual/biennial community. Mean exotic species cover was slightly higher in the untreated areas, and this difference approached significance, but the overall cover values were quite low for all years (<2.5%). Despite these low cover values, *Tragopogon dubius* (yellow salsify), *Verbascum thapsus* (common mullein), *Bromus inermis* (smooth brome) and *Eragrostis curvula* (weeping lovegrass) increased in frequency and the

relative cover of exotic to native forbs and graminoids also increased through time. These patterns may be cause for concern, since a continual build-up of propagules could enable significant invasions in the future.

INTRODUCTION

Throughout the western U.S., fuels treatments such as thinning and burning are being increasingly applied in ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests to reduce overly dense stands and reduce crown fire risk. Several studies have documented significant reductions in fire severity where pre-fire fuels treatments had been conducted (Pollet and Omi, 2002; Finney *et al.*, 2005; Fulé *et al.*, 2012). Reducing the risk of high severity burning in ponderosa pine forests is of particular concern because these ecosystems are poorly adapted to such large-scale stand replacing fires, due to their evolutionary history of frequent, low severity surface fires (Cooper, 1960; Covington and Moore, 1994; Fulé *et al.*, 2003).

Large, stand replacing fires in southwestern ponderosa pine forests are creating novel conditions, and thus future plant community trajectories are not easily predicted. These areas have the potential to convert to persistent shrublands or grasslands (Savage and Mast, 2005), and even if pines do recapture these sites, it could take decades (Haire and McGarigal, 2008, 2010). Plant communities in severely burned areas are likely to remain distinct from those in forested areas for many years (Bataineh *et al.*, 2006) and such changes to native vegetation could have significant ramifications on a number of trophic levels, including herbivores, pollinators, as well as on native wildlife communities (Beier *et al.*, 2008).

Given the predictions for a warmer and drier climate in the Southwest (Seager *et al.*, 2007), these large-scale high severity fire events are likely to continue, which means that fuels treatments are also likely to become more and more prevalent on the landscape. A number of

studies have examined plant community responses to fire severity (Foxy, 1996; Crawford *et al.*, 2001; Griffis *et al.*, 2001; Barclay *et al.*, 2004; Laughlin and Fulé, 2008), or to fuels reduction treatments (Laughlin *et al.*, 2004; Moore *et al.*, 2006; Stoddard *et al.*, 2011). However, few studies have examined post-wildfire plant community response relative to pre-fire treatment (but see Hunter *et al.* 2006 and Kuenzi *et al.* 2008). In addition, most of these previous studies were carried out only in the first few years post-fire, limiting our understanding of post-fire successional change through time (but see Foxy 1996 and Bataineh *et al.* 2006).

The initial floristics hypothesis predicts that post-disturbance plant community dynamics are determined in large part by life history characteristics (Egler, 1954). Under this hypothesis, early post-disturbance communities are dominated by annual/biennial forbs and graminoids that are well suited to the immediate post-disturbance environment. The dominance of these species then give way to the slower growing, later successional species such as perennial herbaceous plants and woody shrubs. Observational studies generally support this hypothesis, at least in terms of the prevalence of annual/biennial species in the early post-fire environment (Keeley *et al.*, 1981; Turner *et al.*, 1997; Crawford *et al.*, 2001; Barclay *et al.*, 2004; Schoennagel *et al.*, 2004; Bataineh *et al.*, 2006; Laughlin and Fulé, 2008; Sabo *et al.*, 2009). Similarly, annual/biennial species can also respond positively to lower-severity disturbances such as prescribed fire (Laughlin *et al.*, 2004; Moore *et al.*, 2006; Sabo *et al.*, 2009), although this response is less consistent, since at least one study did not detect differences between areas that were or were not treated with prescribed fire (Scudieri *et al.*, 2010).

This successional pattern is important in part because some exotic species may fill such opportunistic roles immediately post-fire. Although exotic species exhibit a myriad of plant strategies and tolerances (Martin *et al.*, 2009), many are ruderal, annual or biennial species, that are well adapted to colonizing disturbed areas (Grime, 1977; Sutherland, 2004). In addition,

many exotic species are also shade-intolerant, making severely burned sites more suitable habitat than forests with an intact canopy for these species (Weaver *et al.*, 2001; Sutherland, 2004). A recent review by Moles *et al.* (2012) found that changes to a disturbance regime explained more variation in exotic response than disturbance per se. Ponderosa pine forests of the Southwest have indeed experienced a change in the disturbance regime with the onset of large-scale, high severity fires. Numerous studies have linked high severity fire with exotic species invasions in semi-arid ecosystems (Crawford *et al.*, 2001; Floyd *et al.*, 2006; Dodge *et al.*, 2008; Rew and Johnson, 2010), but others have documented a limited exotic response (Fornwalt *et al.*, 2003; Huisinga *et al.*, 2005; Kuenzi *et al.*, 2008; McMaster, 2010), making predictions about exotic response to fire difficult. In addition to fire severity, disturbances associated with fuels reduction treatments may also facilitate exotic species response (Sieg *et al.*, 2003; Korb *et al.*, 2005; McGlone *et al.*, 2009; Sabo *et al.*, 2009). Increasing our understanding of exotic response to fire and fuels treatments is crucial, because exotic species invasions have the potential to displace native species (Rejmanek *et al.*, 2005) and some can alter future fire regimes (Brooks *et al.*, 2004).

In this study, we examine the effects of pre-fire treatment on plant community response over time. We build on an investigation by Strom and Fulé (2007), who examined the effects of pre-fire treatment on fire severity and post-fire forest structure on the 2002 Rodeo-Chediski fire of east-central Arizona. They observed that the untreated areas were generally severely burned, where there were few surviving overstory trees and the associated near-total loss of canopy cover (Strom and Fulé, 2007). To examine understory plant community response to treatment, we measured understory plant community characteristics in 2004, 2005 and 2011, using a subset of the plots installed by Strom and Fulé (2007). Our objective was to address the following questions:

- 1) How did understory plant community response differ between the pre-fire treated areas that generally burned less severely, and the pre-fire untreated areas that were generally more severely burned? Were these differences consistent through time?
- 2) Did annual/biennial cover decrease relative to perennial cover as expected under the initial floristics hypothesis, and was this pattern more pronounced in the pre-fire untreated areas?
- 3) Was exotic species response stronger in the early post-fire community, or was it persistent through time?

METHODS

Study area

The study area lies south of the Mogollon Rim in east-central Arizona in the Black Mesa and Pinedale Ranger Districts of the Apache-Sitgreaves National Forest. Precipitation by water year was well below the 60-year average for measurement years 2004 and 2011, above average for 2005, and generally below average for the nine years of post-fire vegetation recovery (Figure 1). The average water year precipitation was 45.0 cm, and individual measurement year precipitation was as follows: 31.6 cm in 2004, 54.1 cm in 2005 and 30.6 cm in 2011. Average annual snowfall for 1950-2011 was 102.4 cm. Winter snowfall was significantly lower than the 61-year average for all three measurement years, ranging from approximately 49% of average in the winter of 2003/2004, 22% of average for 2004/2005 and 18% of average for 2010/2011. The maximum average monthly temperature was 29.2° C, which occurred in July and the minimum average monthly temperature was -8.7° C, which occurred in January. Weather data from 1950-2011 recorded at the Heber Ranger Station are available from the Western Regional Climate Center (www.wrcc.dri.edu).

Site selection

We used the same 14 paired sites sampled by Strom and Fulé (2007). The treated sites were originally selected where treatment had occurred within 12 years prior to the fire. The untreated sites were in adjacent untreated areas of similar topography with no natural firebreak between the treated and untreated areas. The treatments were non-commercial thinning, followed by pile burning of the slash (except for one site where slash was lopped and scattered and one where slash was crushed) (Strom and Fulé, 2007). In addition, ongoing fuelwood collection and salvage logging has taken place in some of these areas, as well as intermittent livestock grazing (Gayle Richardson, U.S. Forest Service, Apache-Sitgreaves National Forest, personal communication).

The entire burn area on the Apache-Sitgreaves National Forest was seeded immediately after the wildfire in 2002 and again in 2003. In 2002 the seed mix contained: *Hordeum vulgare* L. (common barley), *Lolium perenne* L. (annual rye), *Elymus trachycaulus* (Link) Gould ex Shinnars (slender wheatgrass), and *Bromus marginatus* Nees ex Steud. (mountain brome) (*B. marginatus* = *B. carinatus* Hook. & Arn. (Welsh *et al.*, 1993)). In 2003 the seed mix where our plots were located contained: *Pascopyrum smithii* (Rydb.) A. Löve (western wheatgrass), *Bouteloua curtipendula* (Michx.) Torr. (sideoats grama), *Festuca ovina* L. (sheep fescue), *Koeleria macrantha* (Ledeb.) J.A. Schultes (prairie junegrass), *Penstemon palmeri* Gray (Palmer's penstemon), and *H. vulgare* (Kuenzi, 2006).

Measurement

We measured overstory structure in 2004 and 2011, and understory plant community characteristics in 2004, 2005 and 2011. Understory characteristics were measured on a subset of the plots established by Strom and Fulé (2007). Each of the 14 sites originally had six subsample

plots, for a total of 42 plots per pre-fire treatment (84 plots total). In 2005 one plot was not re-located, and in 2011 we were unable to re-locate three additional plots, so that two untreated sites had five subsample plots and one site had only four, for a total of 80 plots. We used a variable-radius prism plot (basal area factor 2.3 m²/ha) for overstory trees, on which we recorded the tree species and measured diameter at breast height (DBH, 1.37 m) for each tree in the plot. We used a hemispherical fisheye lens (Nikon CoolPix E4300 and FC-E8 Fisheye Converter Lens) to photograph canopy cover, and analyzed these photographs using the Gap Light Analyzer (Institute of Ecosystem Studies, 1999) to quantify percent canopy openness. In addition, we re-photographed the plot overview to record a series of plot images through time.

We measured understory characteristics using two perpendicular 44.8-m transects to create the 1000-m² plot. Along each transect, we measured plant canopy by six cover classes in ten 20- X 50-cm quadrats, for a total of 20 quadrats per plot (Daubenmire, 1959). Cover data was recorded by life form and nativity as well as by species, including trees shorter than 1.37 m. We estimated cover by species and by life forms separately, so cover of overlapping plants was not counted twice. We estimated cover by life history strategy (annual/biennial, perennial) post-hoc by adding the individual species cover data, so totals may include overlapping plants. Finally, we generated a species occurrence list for the entire plot area.

Plant nomenclature and nativity followed the USDA-NRCS PLANTS Database (USDA-NRCS, 2011). One exception was *Portulaca oleracea* L. (little hogweed), which was listed as “introduced” on the PLANTS database, but along with Kuenzi *et al.* (2008) we classified it as “native” based on Byrne and McAndrews (1975). When we were unable to identify plants to species, we classified them to the lowest taxonomic level we could identify with certainty, generally to the genus level.

Statistical Methods

Since the measurement plots at each site were subsamples, we averaged them to the site level for all analyses (total $n = 14$). We based all plant community analyses on the subset of species that occurred in at least 5% of the plant cover quadrats, and richness analyses on species that occurred on at least 5% of the plot species lists, in order to reduce the influence of uncommon species (McCune and Grace, 2002). We conducted multivariate analyses of plant community differences for each year separately. We analyzed each year with a one-way perMANOVA, a non-parametric permutation procedure, on pre-fire treatment (treated, untreated) in PC-ORD (McCune and Mefford, 1999) using the Bray-Curtis dissimilarity measure with 9999 permutations at an alpha level of 0.05 ($n = 14$).

We graphically displayed the plant community data at the plot level in ordination space, using non-metric multidimensional scaling (NMDS). We conducted 250 runs with real data and 250 runs on randomizations from a random starting point, with an instability criterion of 0.00001. We chose the final number of axes based on stress levels <15 with p -values <0.05 (Peck, 2010). Finally, we used PC-ORD to identify indicator species for each treatment, based on relative frequency and percent cover for each species. Species with an indicator value ≥ 25 and a p -value (based on a Monte Carlo test) < 0.05 were considered indicator species for that treatment (Dufrene and Legendre, 1997). Since we suspected that plant community differences may be related to overstory structure variables, we overlaid tree density, basal area and canopy openness on the multivariate ordinations of the sampling plots.

For all univariate response variables, such as cover by life form and life history strategy, species richness, tree density, canopy openness and basal area, we used a generalized linear model to perform repeated-measures tests on year and treatment in SAS, Version 9.2 (SAS Institute, 1999). Based on inspection of the data, we selected distributions for tree density

(negative binomial), richness (Poisson) and basal area (lognormal). For plant canopy cover data, we used a beta distribution since it is customarily used to model continuous percentages. Because this distribution is not inclusive of the end points (0 or 1), we re-scaled the data to eliminate zero values, using the transformation method described in Smithson and Verkuilen (2006). We evaluated pairwise comparisons for year when the main effect was significant. Where an interaction was significant at $\alpha = 0.05$ (or approached significance at $\alpha \leq 0.10$), we generated post-hoc contrasts for treatment within year, and between years for a given treatment.

RESULTS

We documented the presence of a total of 384 species from 199 genera and 51 families; of these, there were a total of 39 exotic species from 11 families, mostly from Poaceae (14). For multivariate plant community analyses on cover we focused on the 104 species found on at least 5% of the quadrats, and for richness analyses we focused on the 163 species found on at least 5% of the plots, of which 16 were exotic species (Table 1).

Overall plant community response

To assess treatment effects on the overall plant community, we focused on plant composition from species cover data, the related overstory structure variables, species richness and cover by life form. We detected significant differences in plant cover by species between treated and untreated plant communities in 2004 ($p = 0.039$) and 2005 ($p = 0.025$), but this difference waned in 2011 ($p = 0.10$). The ordinations for each year reflect the distinction between treated and untreated plant communities of 2004 and 2005 and the less distinct plant communities in 2011 (Figure 2). The overstory structure variables we overlaid on these

ordinations (basal area, tree density and canopy openness) varied in how they changed between the 2004 and 2011 measurements.

Basal area was significantly lower in untreated areas ($p = 0.0004$) but did not differ by year (Figure 3). Since there were significant treatment-by-year interactions for both tree density and canopy openness (Table 2), we investigated contrasts for treatment differences within years and within treatment through time. Canopy openness was significantly greater in untreated areas in both 2004 ($p = 0.0017$) and 2011 ($p = 0.0007$); however when looking at treatments through time, canopy openness did not differ between years in untreated areas, but the canopy openness decreased from 2004 to 2011 in treated areas ($p = 0.0029$; Figure 3). Tree density was significantly lower in untreated areas in 2004 ($p = 0.0001$) when compared to treated areas. In 2011, this trend reversed in terms of mean tree density, but the difference was not significant ($p = 0.89$, Figure 3). This reversal was driven by one plot each at two of the sites, where the density counts of *Juniperus deppeana* Steud. (alligator juniper) were exceptionally high (271 trees ha^{-1} at one plot and 2,955 trees ha^{-1} on another). Tree density in treated areas did not change significantly between 2004 and 2011 ($p = 1.00$).

Total plant cover was significantly higher in untreated than treated areas, and was highest in 2005 and lowest in 2011, and these differences were also significant (Table 2, Figure 4). We also examined plant cover differences by life form. Since the treatment-by-year interaction was significant for tree regeneration cover, we conducted post-hoc contrasts and found significantly higher cover in untreated areas in 2011 over 2004 ($p = 0.0054$) and 2005 ($p = 0.0018$). Mean shrub cover was higher in untreated areas, although this difference only approached significance ($p = 0.058$); however, mean shrub cover increased through time and in 2011 was significantly higher than in 2004 and 2005 (Table 2, Figure 4). Shrub species dominance shifted from slightly higher cover of *Ceanothus fendleri* A. Gray (Fendler's ceanothus)

over *Arctostaphylos pungens* Kunth (pointleaf manzanita) in 2004, to five times greater cover of *A. pungens* relative to *C. fendleri* in 2011.

Forb cover was significantly higher in untreated areas ($p = 0.0046$). This was driven primarily by four annual or annual/biennial species, *Bahia dissecta* (A. Gray) Britton (ragleaf bahia), *Chenopodium graveolens* Willd. (fetid goosefoot), *Conyza canadensis* (L.) Cronquist (Canadian horseweed) and *Polygonum douglasii* Greene (Douglas' knotweed), as well as the perennial *Heliomeris multiflora* Nutt. (showy goldeneye). *H. multiflora* was an indicator species of untreated areas for all three years. Forb cover was also significantly different for all years, where the mean trend followed that of total cover (highest in 2005, lowest in 2011). Forb species with the highest cover values generally followed this trend with the exception of annual species *P. douglasii* and *C. graveolens*, which steadily declined over time.

Graminoids also followed this general pattern of mean cover over time (highest in 2005, lowest in 2011), and this difference was significant among all years. Of the individual graminoid species, only the annual *Muhlenbergia minutissima* (Steud.) Swallen (annual muhly), consistently declined in cover over the years. Of the higher cover graminoid species ($>1\%$), the seeded *B. carinatus* did increase in 2005 but declined much more markedly in 2011 than the other graminoids, to $<0.1\%$. Although mean graminoid cover was slightly higher for untreated areas, this difference was not significant ($p = 0.44$).

Overall species richness was not significantly different by treatment, but was significantly higher in 2005 than 2004 ($p = 0.0011$). The indicator species for each treatment varied through time (Table 3). As noted above, the only consistent indicator species for all three years was the perennial forb *H. multiflora* for untreated areas. The untreated areas had more indicator species than treated areas, including one seeded species (*B. carinatus*) in 2005, and one exotic species, *Tragopogon dubius* Scop. (yellow salsify), in 2011. Treated sites had no

indicators for 2004, the seeded perennial grass, *K. macrantha*, for 2005, and the perennial forb, *Packera neomexicana* (A. Gray) W.A. Weber & Á. Löve (New Mexico groundsel), for 2011.

Annual/biennial and perennial response

Mean annual/biennial cover (both forbs and graminoids) was significantly lower in 2011 than in the previous measurements, and the higher mean response in untreated areas approached significance ($p = 0.073$) (Figure 5, Table 2). Perennial plant cover was significantly higher in untreated than treated areas, and also significantly different for each year. The ratio of perennial cover to annual/biennial cover changed dramatically over time, from the 2004 ratios 1.6:1 and 1.7:1 in untreated and treated areas, respectively, to 9.0:1 and 10.4:1 in 2011 (Figure 5). The changes in annual/biennial cover relative to perennial cover was not markedly more pronounced in the untreated areas, but the perennials to annual/biennial ratio was slightly lower in the untreated areas. For all years and both treatments, the majority of annual plant cover was from forb species, but the majority of perennial cover was from graminoid species.

Exotic species response

Exotic forb cover was significantly higher in 2005 than in 2004 or 2011, and the higher mean exotic forb cover in untreated areas approached significance ($p = 0.071$) (Figure 6, Table 4). Mean exotic forb cover values for all years were consistently low, <2.5%. Exotic graminoid cover did not differ significantly by treatment or among years, and mean cover values were all <1%. Exotic species richness was not significantly different among years, but higher mean exotic species richness in untreated areas approached significance ($p = 0.071$) (Figure 5, Table 4). Mean exotic species richness was more similar between treatments in 2004 and 2005, but was somewhat higher in untreated areas (4.9) versus treated areas (3.0) in 2011.

In addition to cover, we also examined turnover of exotic species in terms of frequency (presence/absence by plot) (Table 1). Several exotic forb species decreased between 2004 and

2011, including *Chenopodium album* L. (lambsquarters), *Cirsium vulgare* (Savi) Ten. (bull thistle), and *Lactuca serriola* L. (prickly lettuce). We note that identification uncertainties may confuse the trend for *C. album*. This species may have still been present in 2011, but along with Huisinga *et al.* (2005), the *Chenopodium* plants we encountered were juveniles that were not distinguishable from native *Chenopodium* species. If we were to assume our *Chenopodium* species were indeed *C. album*, then there was still an overall decrease from 34 of 80 plots in 2004 and 15 of 80 plots in 2011. *Verbascum thapsus* L. (common mullein) and *Taraxacum officinale* F.H. Wigg. (common dandelion) frequency remained relatively constant, although mean *V. thapsus* cover increased slightly through time in untreated areas. *T. dubius* had the greatest consistent increase in frequency through time, from 37 of 80 plots in 2004 to 49 of 80 plots in 2011, although overall cover changes were minimal.

Exotic graminoid species decreasing in frequency between 2004 and 2011 were the annuals *Bromus arvensis* L. (field brome) and *Bromus tectorum* L. (cheatgrass), despite the slight increase in *B. tectorum* frequency in 2005. The perennial grasses *Poa pratensis* L. (Kentucky bluegrass) decreased while *Poa compressa* L. (Canada bluegrass) increased, but we suspect there may have been identification errors between these similar species; when combined, there was an increase from 10 to 26 of 80 plots. In addition, two other perennial grass species strongly increased in frequency. The strongly rhizomatous *Bromus inermis* Leyss. (smooth brome) increased from 4 to 19 of 80 plots, and *Eragrostis curvula* (Shrad.) Nees (weeping lovegrass) was first detected in 2011 on a total of 18 of 80 plots. Of the two exotic species seeded as part of the post-fire rehabilitation effort the annual *L. perrene* was detected in early years, but was absent from any plots by 2011. In contrast, the seeded perennial *F. ovina* was first detected on 2 plots in 2011.

DISCUSSION

Overall plant community response

Plant community composition by species cover data was distinct between pre-fire treated and untreated areas in 2004 and 2005 but not in 2011, and ordinations reflected this trend toward convergence. We suspected that the differences in the plant communities were driven by overstory structure differences, yet these overstory structure variables did not change much through time, with the exception of slightly less canopy openness in treated areas and increased tree density in untreated areas (which was driven by two plots). Since the relative differences between these plant communities did change, other factors likely influenced this convergence through time.

We speculate that our study design may be one of these factors. First, unlike some of the high severity burn areas sampled on the White Mountain Apache Tribal lands (Chapter 3), the Apache-Sitgreaves National Forest study design is based on paired sites, where the untreated areas are all in close proximity to areas that burned less severely. This proximity likely facilitated faster colonization than may have occurred in the interior of larger high severity burn patches (Turner *et al.*, 1998). However, the convergence in the understory herbaceous communities is only part of the picture. The lack of overstory structure and shrub dominance still indicate a different overall vegetation community compared to the treated areas, when considering all strata.

We also suspect that our sampling protocols, which were adequate in 2004 and 2005, may have underestimated the regeneration of several important tree species in 2011. Our cover transects only sampled tree regeneration under breast height, because of the intention to sample species defined as trees, that are also above breast height, in the variable radius plots. Several important species in this community are sprouting species that are considered trees as

adults but have a shrub-like habit during early growth stages (such as *Quercus gambelii* Nutt. (Gambel oak), *J. deppeana*, and *Robinia neomexicana* A. Gray (New Mexico locust)), as shown in the photographs in Figure 7. Because many of these species were over breast height in 2011, they were not included in our understory cover estimates. However, because of their shrub-like habit at this stage of growth, the small diameter leaders were rarely included in the variable radius plots, and thus this component of the vegetation community was probably under-represented in our results. If these species had been included in the quadrat cover estimates, this may have resulted in a significantly different plant community in 2011. Alternatively, if they had been accounted for in the overstory structure estimates, we may have detected greater and clearer trends in the overstory data used as vectors. We recommend an additional protocol to estimate this intermediate stratum in the future. Despite these caveats, in terms of future trajectories of these severely burned, untreated areas, it is encouraging that the understory herbaceous community is becoming more similar to that of the less severely burned, treated areas.

We detected consistently higher total plant cover in the more severely burned areas, similar to patterns observed by Baitenah *et al.* (2006). Over time, mean total plant cover and cover by life form increased between 2004 and 2005, when higher plant cover in untreated areas was mostly forb species. The dramatic decrease in total plant, forb and graminoid cover in 2011 may be related to competitive effects from increasing shrub cover on the untreated sites. The continual increase in shrub cover may be due to the slower-growing strategy of many shrub species that are likely to become stronger competitors later in time. Whereas *A. pungens* dominated the 2011 shrub community, *C. fendleri* was more strongly established in the first years post-fire, which may be related to heat-stimulated germination (Huffman and Moore, 2004).

In addition to competition with shrubby species, several other factors are likely related to the dramatic decrease in forb and graminoid cover in 2011. First, droughty conditions in the years post-fire (Figure 1) likely further suppressed herbaceous response over time. Many studies in the Southwest have detected decreases in cover which they have linked with persistent drought (Bataineh *et al.*, 2006; Moore *et al.*, 2006). Second, herbaceous plants can respond positively to nitrogen pulses that occur in the first few years post-fire (Esque *et al.*, 2010), and it is possible that the higher cover on our sites was responding to some degree to increased nutrient availability in 2004 and 2005 that may have been unavailable in 2011. Third, intermittent grazing in the area by both livestock and wild ungulates may also have reduced understory cover, but detailed records of grazing history were unavailable.

Annual/perennial response

The first interesting trend in annual/biennial forb and graminoid cover was higher mean annual/biennial cover in the untreated areas. Although this difference only approached significance, it is consistent with our expectations of a greater ruderal response in more heavily disturbed areas. It may also be related to the ongoing fuelwood collection and salvage logging that has taken place in some of these areas, which has likely created an ongoing, low-intensity disturbance.

The second finding is that annual/biennial cover decreased relative to perennial species over time. In untreated areas, this offers general support for Egler's initial floristics hypothesis, and emphasizes the importance of life history strategies in trends of secondary succession (Egler, 1954). In treated areas that were not set back to such an early seral stage, the post-fire response was similar to that observed in other ponderosa pine forests with more open stand structures that burned less severely. Moore *et al.* (2006) observed an increase in the standing crop of annuals/biennial forbs in thinned ponderosa pine stands that had forest floor

manipulation and burning, followed by a subsequent decline. In addition, in two studies from the North Rim of the Grand Canyon found increases in annual/biennial forb richness (Laughlin *et al.*, 2004) as well as increases in annual/biennial forbs and grass cover (Laughlin and Fulé, 2008) in the first few years post-fire.

Exotic species cover and richness

Exotic species response was not limited to a ruderal, immediate post-fire role. In general, the exotic response was quite low ($\leq 2.5\%$ for all years) and highly variable, making the comparison of trends by life history strategy interesting, but not definitive. One general trend worth reporting, despite these limitations, is the higher proportion of mean exotic annual/biennial cover relative to native annual/biennial cover in 2011, particularly in untreated areas. This may suggest that the annual/biennial exotic species are more persistent than the native annual/biennial species through time.

When considering exotic cover by life form, exotic forb cover was significantly higher in 2005 than either of the other two years. These species were likely responding to increased moisture in 2005 and to droughty conditions in 2011, just as native forbs were. This is consistent with studies that demonstrate that exotic species generally respond to the same environmental conditions as native species (Meiners, 2007), although exotic graminoids did not show any consistent trend.

The low overall exotic response on our sites is consistent with some other studies on high severity fires in the region (Fox, 1996; Huisinga *et al.*, 2005; Kuenzi *et al.*, 2008; McMaster, 2010). With the exception of Kuenzi *et al.* (2008), many of these areas were not as heavily managed as our study sites, which have been subjected to grazing, recreation, logging and road-building (Kuenzi, 2006). When this is coupled with disturbance, our results are somewhat surprising as a number of studies have documented exotic species invasions in severely burned

ponderosa pine forests (Crawford *et al.*, 2001; Griffis *et al.*, 2001; Barclay *et al.*, 2004; Dodge *et al.*, 2008). However, it is problematic to compare the exotic response in our study to other studies in this region, because of differences in species classification. Some studies do not provide lists of observed exotic species (Griffis *et al.*, 2001), and still others classified species such as *Conyza canadensis* (L.) Cronquist (Canadian horseweed) as exotic (Crawford *et al.*, 2001; Barclay *et al.*, 2004), which we consider native based on the USDA Plants database (USDA-NRCS, 2011), local floras (Kearney *et al.*, 1961) and field guides (Springer *et al.*, 2009).

Despite the overall low cover values we observed, there may be some cause for concern about exotic species on these sites. First, we detected an increase in the amount of exotic cover relative to overall cover by life form in untreated areas. The portion of exotic forb cover that comprises the overall forb cover increased from 1.6% in 2004 to 7.9% in 2011; relative exotic graminoid cover increases were slightly smaller, from 4.2% in 2004 to 5.9% in 2011. Although these numbers are not exceptionally large, these increases may allow exotic species to build up enough propagule pressure to facilitate a stronger invasion following another, future disturbance event, or significant precipitation (McGlone *et al.*, 2009).

The increase in frequency of certain exotic species through time also raises concerns. An experimental study in semi-arid sagebrush ecosystems found that *T. dubius*, a deeply tap-rooted perennial forb, could out-compete native grasses after disturbance due to its ability to access deep water resources that were available after the loss of the foundation species (Prevey *et al.*, 2010a; Prevey *et al.*, 2010b). This species was an indicator species in 2011 and had the greatest increase in frequency on untreated sites during our study; since droughty conditions are expected to continue in the Southwest (Seager *et al.*, 2007), this species may further proliferate in the future. Finally, the appearance of the exotic perennial bunchgrass, *E. curvula*, in 2011 may also be of concern. This species was seeded on the Dude Fire, and remained the dominant cover

(93%) 15 years post-fire, suggesting it can persist on the landscape (Leonard, 2007). In addition, it responds well to burning (McFarland and Mitchell, 2000), and since it is now established in the area, future fires may greatly increase the presence of this species on the local landscape.

CONCLUSIONS

There is now a substantial body of research on exotic species invasions after severe fire in the Southwest, yet no clear patterns have emerged. Studies have found varying rates of invasion on landscapes that both were and were not heavily managed (disturbed pre-fire). Given the differences in exotic species composition and abundance across such fires, local site-specific factors are likely driving exotic response. Although the disturbance of high severity fire can open up growing space for exotic species, on-site propagules, post-fire management practices and weather patterns may be the more important drivers of exotic response.

Our data dosuggest that even if exotic species do not heavily invade such an intensely disturbed ecosystem immediately post-fire, they have the potential to increase over time. These sites should be monitored for further increases in exotic cover, since they are at risk for heavier invasions in the future. In addition, many of the exotic species we observed have been either seeded as part of post-fire rehabilitation or otherwise intentionally introduced (*E. curvula*, *P. pratensis*, *Melilotus officinalis* (L.) Lam. (sweetclover), *D. glomerata*) (Fowler *et al.*, 2008; Wolfson and Sieg, In prep); more generally, since seed mixes can be contaminated with exotic species, past seeding practices in the area may have introduced some of the exotics we detected (Fowler *et al.*, 2008; Peppin *et al.*, 2010). Seeding exotic species in the future is not recommended, and even native seed should be applied with caution due to the potential for exotic seed contamination.

Finally, Strom and Fulé (2007) detected significant reductions in fire severity in areas treated before the Rodeo-Chediski Fire, and our data show that those treatments also had a persistent effect on vegetation response nine years post-fire. Our data suggest that pre-fire treatments can help maintain native plant communities associated with an intact ponderosa pine forest.

REFERENCES

- Barclay, A.D., Betancourt, J.L., Allen, C.D., 2004. Effects of seeding ryegrass (*Lolium multiflorum*) on vegetation recovery following fire in a ponderosa pine (*Pinus ponderosa*) forest. *International Journal of Wildland Fire* 13, 183-194.
- Bataineh, A.L., Oswald, B.P., Bataineh, M.M., Williams, H.M., Coble, D.W., 2006. Changes in understory vegetation of a ponderosa pine forest in northern Arizona 30 years after a wildfire. *Forest Ecology and Management* 235, 283-294.
- Beier, P., Rogan, E.C., Ingraldi, M.F., Rosenstock, S.S., 2008. Does forest structure affect reproduction of northern goshawks in ponderosa pine forests? *Journal of Applied Ecology* 45, 342-350.
- Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677-688.
- Byrne, R., McAndrews, J.H., 1975. Pre-Columbian Purslane (*Portulaca-Oleracea* L) in New World. *Nature* 253, 726-727.
- Cooper, C.F., 1960. Changes in vegetation, structure, and growth of south-western pine forests since white settlement. *Ecological Monographs* 30, 130-164.
- Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa forest structure - changes since Euro-American settlement. *Journal of Forestry* 92, 39-47.
- Crawford, J.S., Wahren, C.H.A., Kyle, S., Moir, W.H., 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *Journal of Vegetation Science* 12, 261-268.
- Daubenmire, R.F., 1959. A canopy-coverage method. *Northwest Science* 33, 43-64.
- Dodge, R.S., Fulé, P.Z., Sieg, C.H., 2008. Dalmatian toadflax (*Linaria dalmatica*) response to wildfire in a southwestern USA forest. *Ecoscience* 15, 213-222.
- Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67, 345-366.
- Egler, R.E., 1954. Vegetation science concepts I. Initial floristic composition: A factor in old-field vegetation development. *Vegetatio* 4, 412-417.
- Esque, T.C., Kaye, J.P., Eckert, S.E., DeFalco, L.A., Tracy, C.R., 2010. Short-term soil inorganic N pulse after experimental fire alters invasive and native annual plant production in a Mojave Desert shrubland. *Oecologia* 164, 253-263.
- Finney, M.A., McHugh, C.W., Grenfell, I.C., 2005. Stand- and landscape-level effects of prescribed burning on two Arizona wildfires. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 35, 1714-1722.

- Floyd, M.L., Hanna, D., Romme, W.H., Crews, T.E., 2006. Predicting and mitigating weed invasions to restore natural post-fire succession in Mesa Verde National Park, Colorado, USA. *International Journal of Wildland Fire* 15, 247-259.
- Fornwalt, P.J., Kaufmann, M.R., Huckaby, L.S., Stoker, J.A., Stohlgren, T.J., 2003. Non-native plant invasions in managed and protected ponderosa pine Douglas-fir forests of the Colorado Front Range. *Forest Ecology and Management* 177, 515-527.
- Fowler, J.F., Sieg, C.H., Dickson, B.G., Saab, V., 2008. Exotic plant species diversity: Influence of roads and prescribed fire in Arizona ponderosa pine forests. *Rangeland Ecology & Management* 61, 284-293.
- Fox, T.S., 1996. Vegetation succession after the La Mesa fire at Bandelier National Monument. In: Allen, C.D. (Ed.), *Fire Effects in Southwestern Forests: Proceedings of the Second La Mesa Fire Symposium*, 29-31 March 1994. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, Los Alamos, NM, pp. 47-69.
- Fulé, P.Z., Crouse, J.E., Roccaforte, J.P., Kalies, E.L., 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *Forest Ecology and Management* 269, 68-81.
- Fulé, P.Z., Heinlein, T.A., Covington, W.W., Moore, M.M., 2003. Assessing fire regimes on Grand Canyon landscapes with fire-scar and fire-record data. *International Journal of Wildland Fire* 12, 129-145.
- Griffis, K.L., Crawford, J.A., Wagner, M.R., Moir, W.H., 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. *Forest Ecology and Management* 146, 239-245.
- Grime, J.P., 1977. Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111, 1169-1194.
- Haire, S.L., McGarigal, K., 2008. Inhabitants of landscape scars: Succession of woody plants after large, severe forest fires in Arizona and New Mexico. *Southwestern Naturalist* 53, 146-161.
- Haire, S.L., McGarigal, K., 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. *Landscape Ecology* 25, 1055-1069.
- Huffman, D.W., Moore, M.M., 2004. Responses of Fendler ceanothus to overstory thinning, prescribed fire, and drought in an Arizona ponderosa pine forest. *Forest Ecology and Management* 198, 105-115.
- Huisinga, K.D., Laughlin, D.C., Fulé, P.Z., Springer, J.D., McGlone, C.M., 2005. Effects of an intense prescribed fire on understory vegetation in a mixed conifer forest. *Journal of the Torrey Botanical Society* 132, 590-601.

Hunter, M.E., Omi, P.N., Martinson, E.J., Chong, G.W., 2006. Establishment of non-native plant species after wildfires: effects of fuel treatments, abiotic and biotic factors, and post-fire grass seeding treatments. *International Journal of Wildland Fire* 15, 271-281.

Institute of Ecosystem Studies, 1999. Gap Light Analyzer (Computer Program). Simon Fraser University <http://www.ecostudies.org/gla>.

Kearney, T.H., Peebles, R.H., Howell, H.T., McClintok, E., 1961. *Arizona Flora*. University of California Press, Berkeley, CA.

Keeley, S.C., Keeley, J.E., Hutchinson, S.M., Johnson, A.W., 1981. Postfire succession of the herbaceous flora in southern-California chaparral. *Ecology* 62, 1608-1621.

Korb, J.E., Springer, J.D., Powers, S.R., Moore, M.M., 2005. Soil seed banks in *Pinus ponderosa* forests in Arizona: Clues to site history and restoration potential. *Applied Vegetation Science* 8, 103-112.

Kuenzi, A.M., 2006. Pre-fire treatment effects and understory plant community response on the Rodeo-Chediski fire, Arizona. M.S. Thesis, School of Forestry, Flagstaff, AZ, Northern Arizona University.

Kuenzi, A.M., Fulé, P.Z., Sieg, C.H., 2008. Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. *Forest Ecology and Management* 255, 855-865.

Laughlin, D.C., Bakker, J.D., Stoddard, M.T., Daniels, M.L., Springer, J.D., Gildar, C.N., Green, A.M., Covington, W.W., 2004. Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. *Forest Ecology and Management* 199, 137-152.

Laughlin, D.C., Fulé, P.Z., 2008. Wildland fire effects on understory plant communities in two fire-prone forests. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 38, 133-142.

Leonard, J.M., 2007. The influence of parent material on vegetation response 15 years after the Dude Fire, Arizona. M.S. Thesis, School of Forestry, Flagstaff, AZ Northern Arizona University.

Martin, P.H., Canham, C.D., Marks, P.L., 2009. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology and the Environment* 7, 142-149.

McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., Mefford, M.J., 1999. *PC-ORD (Computer Software)*. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, OR.

McFarland, J.B., Mitchell, R., 2000. Fire effects on weeping lovegrass tiller density and demographics. *Agronomy Journal* 92, 42-47.

McGlone, C.M., Springer, J.D., Laughlin, D.C., 2009. Can pine forest restoration promote a diverse and abundant understory and simultaneously resist nonnative invasion? *Forest Ecology and Management* 258, 2638-2646.

McMaster, M.A., 2010. Effects of fire and post-fire seeding on plant communities in a ponderosa pine forest. M.S. Thesis, School of Forestry, Flagstaff, AZ, Northern Arizona University.

Meiners, S.J., 2007. Native and exotic plant species exhibit similar population dynamics during succession. *Ecology* 88, 1098-1104.

Moles, A.T., Flores-Moreno, H., Bonser, S.P., Warton, D.I., Helm, A., Warman, L., Eldridge, D.J., Jurado, E., Hemmings, F.A., Reich, P.B., Cavender-Bares, J., Seabloom, E.W., Mayfield, M.M., Sheil, D., Djietror, J.C., Peri, P.L., Enrico, L., Cabido, M.R., Setterfield, S.A., Lehmann, C.E.R., Thomson, F.J., 2012. Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology* 100, 116-127.

Moore, M.M., Casey, C.A., Bakker, J.D., Springer, J.D., Fulé, P.Z., Covington, W.W., Laughlin, D.C., 2006. Herbaceous vegetation responses (1992-2004) to restoration treatments in a Ponderosa pine forest. *Rangeland Ecology & Management* 59, 135-144.

Peck, J.E., 2010. *Multivariate Analysis for Community Ecologists: Step-by-Step using PC-ORD*. MjM Software Design, Gleneden Beach, OR.

Peppin, D., Fulé, P.Z., Sieg, C.H., Beyers, J.L., Hunter, M.E., 2010. Post-wildfire seeding in forests of the western United States: An evidence-based review. *Forest Ecology and Management* 260, 573-586.

Pollet, J., Omi, P.N., 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *International Journal of Wildland Fire* 11, 1-10.

Prevey, J.S., Germino, M.J., Huntly, N.J., 2010a. Loss of foundation species increases population growth of exotic forbs in sagebrush steppe. *Ecological Applications* 20, 1890-1902.

Prevey, J.S., Germino, M.J., Huntly, N.J., Inouye, R.S., 2010b. Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. *Plant Ecol.* 207, 39-51.

Rejmanék, M., Richardson, D.M., Higgins, S.I., Pitcairn, M.J., Grotkopp, E., 2005. Ecology of Invasive Plants: State of the Art. In: Mooney, H.A., Mack, R.N., McNeely, J.A., Neville, L.E., Schei, P.J., Waage, J.K. (Eds.), *Invasive Alien Species: A New Synthesis*.

Rew, L.J., Johnson, M.P., 2010. Reviewing the Role of Wildfire on the Occurrence and Spread of Invasive Plant Species in Wild land Areas of the Intermountain Western United States. *Invasive Plant Science and Management* 3, 347-364.

Sabo, K.E., Sieg, C.H., Hart, S.C., Bailey, J.D., 2009. The role of disturbance severity and canopy closure on standing crop of understory plant species in ponderosa pine stands in northern Arizona, USA. *Forest Ecology and Management* 257, 1656-1662.

- SAS Institute, 1999. The SAS System, Version 8.02. In: SAS Institute, Inc., Cary, NC.
- Savage, M., Mast, J.N., 2005. How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 35, 967-977.
- Schoennagel, T., Waller, D.M., Turner, M.G., Romme, W.H., 2004. The effect of fire interval on post-fire understorey communities in Yellowstone National Park. *Journal of Vegetation Science* 15, 797-806.
- Scudieri, C.A., Sieg, C.H., Haase, S.M., Thode, A.E., Sackett, S.S., 2010. Understory vegetation response after 30 years of interval prescribed burning in two ponderosa pine sites in northern Arizona, USA. *Forest Ecology and Management* 260, 2134-2142.
- Seager, R., Ting, M.F., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.P., Harnik, N., Leetmaa, A., Lau, N.C., Li, C.H., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316, 1181-1184.
- Sieg, C.H., Phillips, B.G., Moser, L.P., 2003. Exotic invasive plants. In: Frederici, P. (Ed.), *Ecological Restoration of Southwestern Ponderosa Pine Forests*. Island Press, Washington, DC, pp. 251-267.
- Smithson, M., Verkuilen, J., 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods* 11, 54-71.
- Springer, J.D., Daniels, M.L., Nazaire, M., 2009. *Field Guide to Forest and Mountain Plants of Northern Arizona*. Ecological Restoration Institute, Flagstaff, AZ.
- Stoddard, M.T., McGlone, C.M., Fulé, P.Z., Laughlin, D.C., Daniels, M.L., 2011. Native plants dominate understory vegetation following ponderosa pine forest restoration treatments. *Western North American Naturalist* 71, 206-214.
- Strom, B.A., Fulé, P.Z., 2007. Pre-wildfire fuel treatments affect long-term ponderosa pine forest dynamics. *International Journal of Wildland Fire* 16, 128-138.
- Sutherland, S., 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. *Oecologia* 141, 24-39.
- Turner, M.G., Romme, W.H., Gardner, R.H., Hargrove, W.W., 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67, 411-433.
- Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. *Ecosystems* 1, 511-523.
- USDA-NRCS, 2011. The PLANTS Database (<http://plants.usda.gov>, 15 November 2011). In: National Plant Data Center, Baton Rouge, LA 70874-4490, USA.

Weaver, T., Gusafson, D., Lichthardt, J., 2001. Exotic plants in early and late seral vegetation of fifteen northern Rocky Mountain environments (HTs). *Western North American Naturalist* 61, 417-427.

Welsh, S.L., Atwood, N.D., Goodrich, S., Higgins, L.C., 1993. *A Utah Flora*. Brigham Young University, Provo, UT.

Wolfson, B.A.S., Sieg, C.H., In prep. 40-year post fire seeding trends in Arizona and New Mexico. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Table 1. Exotic species by number of plots (out of a total of 80) and year. Species in bold are those found on at least 5% of the total number of plots when all years are combined (i.e. 240). Species life history strategies are abbreviated as A: annual, B: biennial and P: perennial.

	Species	Life History	2004	2005	2011
<i>Forbs</i>	<i>Amaranthus blitoides</i>	A	1		
	<i>Bassia hyssopifolia</i>	A		1	
	<i>Bassia scoparia</i>	A	1		
	<i>Chenopodium album</i>	A	34	5	
	<i>Chenopodium botrys</i>	A	4		
	<i>Cirsium vulgare</i>	B	19	24	10
	<i>Erodium cicutarium</i>	A	15	14	13
	<i>Lactuca serriola</i>	P	43	59	36
	<i>Malva neglecta</i>	ABP	1	2	1
	<i>Medicago lupulina</i>	P	2	3	5
	<i>Medicago sativa</i>	P	1	2	
	<i>Melilotus officinalis</i>	P	7	7	11
	<i>Polygonum aviculare</i>	AP	4	5	1
	<i>Polygonum convolvulus</i>	A		1	
	<i>Rorippa sylvestris</i>	P		1	1
	<i>Rumex acetosella</i>	P	3	2	1
	<i>Rumex crispus</i>	P	2	1	1
	<i>Salsola tragus</i>	A	1	1	
	<i>Sanguisorba minor</i>	P	1	2	
	<i>Sisymbrium altissimum</i>	AB		3	3
	<i>Sonchus sp.</i>	P		4	
	<i>Taraxacum officinale</i>	P	21	23	20
	<i>Tragopogon dubius</i>	AB	37	45	49
	<i>Verbascum thapsus</i>	B	47	51	48
<i>Graminoids</i>	<i>Agropyron desertorum</i>	P		2	
	<i>Avena fatua</i>	A		1	
	<i>Bromus inermis</i>	P	4	6	19
	<i>Bromus japonicas</i>	A	9	7	5
	<i>Bromus racemosus</i>	A		1	
	<i>Bromus tectorum</i>	A	11	23	16
	<i>Dactylis glomerata</i>	P	2	3	1
	<i>Echinochloa crus-galli</i>	A		1	
	<i>Eragrostis curvula</i>	P			18
	<i>Festuca ovina</i>	P			1
	<i>Lolium perenne</i>	AP	24	10	
	<i>Poa compressa</i>	P		11	23
	<i>Poa pratensis</i>	P	10	4	3
	<i>Schedonorus pratensis</i>	P		3	
	<i>Triticum aestivum</i>	A	12	2	

Table 2. P-values for year, treatment and interaction for univariate variables, including total cover, cover by lifeform and richness. Where year was significant, we included the p-values for pairwise comparisons. All p-values are given to two significant digits.

Variable	Year	Treatment	Interaction
Total cover	0.0001*	0.0011*	0.73
2004-2005	0.047*		
2004-2011	0.0004*		
2005-2011	0.0002*		
Tree regeneration cover	0.0091*	0.27	0.02*
2004-2005	0.0001*		
2004-2011	0.0001*		
2005-2011	0.0001*		
Shrub cover	0.029*	0.058	0.72
2004-2005	0.041*		
2004-2011	0.041*		
2005-2011	0.40		
Forb cover	0.0001*	0.0046	0.72
2004-2005	0.0059*		
2004-2011	0.0001*		
2005-2011	0.0001*		
Graminoid cover	0.0001*	0.44	0.94
2004-2005	0.0007*		
2004-2011	0.0001*		
2005-2011	0.0001*		
Annual/Biennial cover	0.0001*	0.073	0.51
2004-2005	0.18		
2004-2011	0.20		
2005-2011	0.0001*		
Perennial cover	0.0001*	0.0048*	0.17
2004-2005	0.0001*		
2004-2011	0.0001*		
2005-2011	0.0001*		
Richness	0.0037*	0.19	0.21
2004-2005	0.0024*		
2004-2011	0.69		
2005-2011	0.98		

Table 3. Indicator species by treatment and year.

	2004	2005	2011
Untreated	<i>Bahia dissecta</i>	<i>Bromus carinatus</i> ^a	<i>Cirsium wheeleri</i>
	<i>Erigeron divergens</i>	<i>Erigeron divergens</i>	<i>Epilobium brachycarpum</i>
	<i>Eriogonum racemosum</i>	<i>Heliomeris multiflora</i>	<i>Heliomeris multiflora</i>
	<i>Heliomeris multiflora</i>	<i>Juniperus depeanna</i>	<i>Tragopogon dubius</i> ^b
	<i>Packera neomexicana</i>		
Treated	<i>none</i>	<i>Koeleria macrantha</i> ^a	<i>Packera neomexicana</i>

^a Species seeded after the Rodeo-Chediski Fire on the Apache-Sitgreaves National Forest in 2002 and 2003.

^b Exotic species.

Table 4. P-values for year, treatment and the interaction for exotic cover and richness. We included the p-values for pairwise comparisons among years where the main effect was significant.

Variable	Year	Treatment	Interaction
Exotic forb cover	0.0039*	0.071	0.97
<i>2004-2005</i>	<i>0.0023*</i>		
<i>2004-2011</i>	<i>0.87</i>		
<i>2005-2011</i>	<i>0.016*</i>		
Exotic graminoid cover	0.60	0.67	0.51
Exotic richness	0.28	0.071	0.18

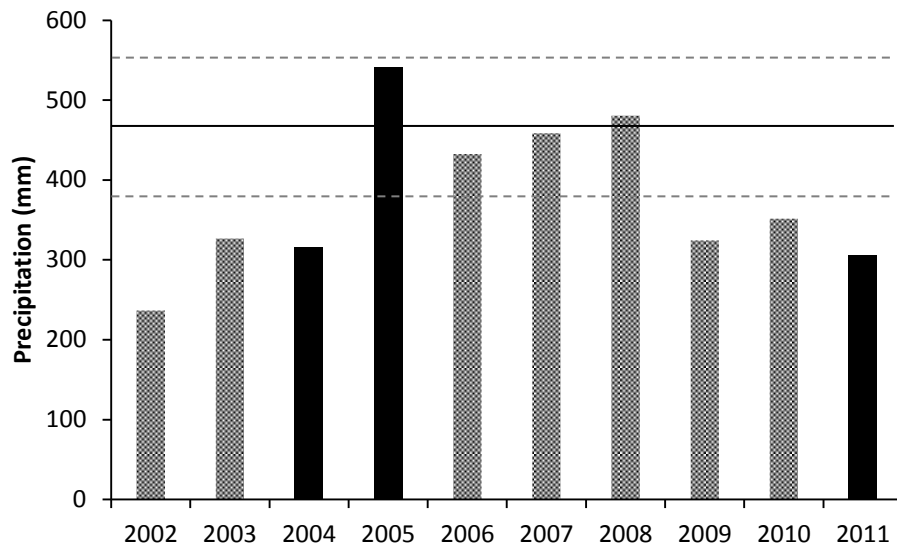
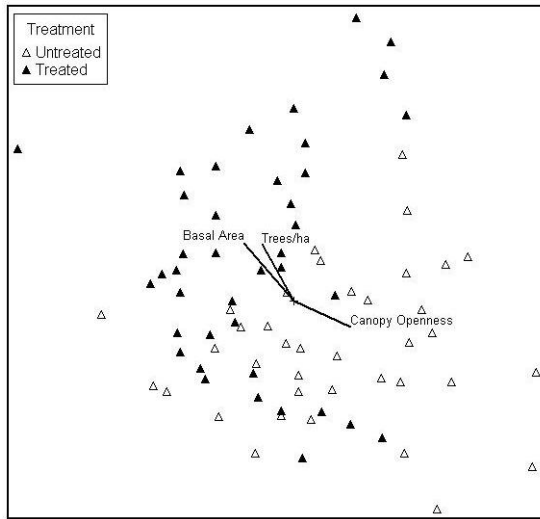
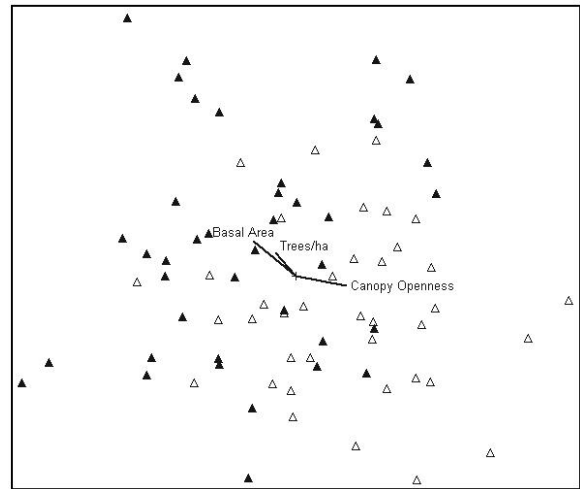


Figure 1. Precipitation data by water year from the Heber Ranger Station, Heber, AZ. Water year for a given year includes October through December of the previous year, and January through September of that year. The black line represents the 60-year average, and the grey dashed lines are one standard deviation. Solid black bars denote measurement years.

(a) 2004



(b) 2005



(c) 2011

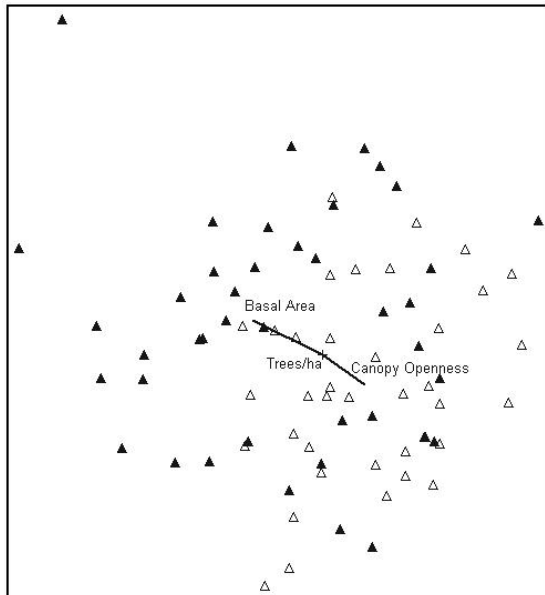


Figure 2. NMDS ordinations showing communities at the plot-level for each year with basal area, tree density and canopy openness overlaid as vectors. Vectors in the ordinations for 2004 (a) and 2005 (b) both use 2004 stand structure data, and show 78 of our 80 plots since canopy openness data was missing from two plots. 2011 ordination (c) uses 2011 stand structure data, and show 79 of our 80 plots, also due to missing canopy data. Stress levels and final dimensionality are: (a) 2004: 15.81, 4 dimensions; (b) 2005: 15.93, 4 dimensions; (c) 2004: 15.60, 4 dimensions.

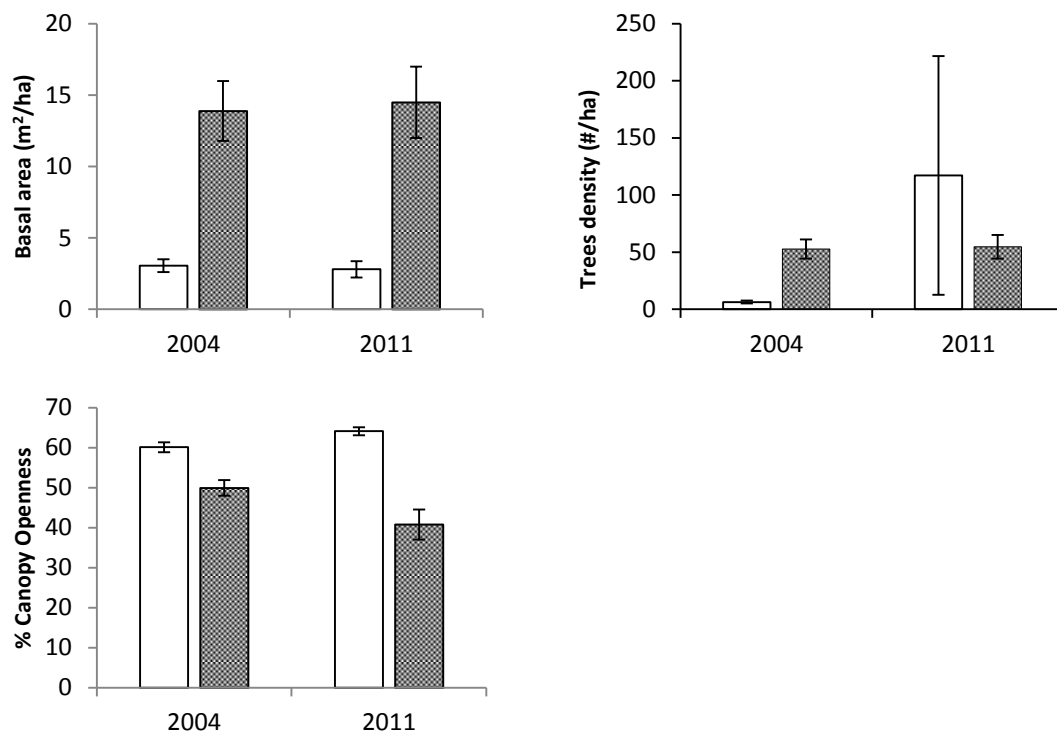


Figure 3. Basal area and tree density from variable-radius prism plots (basal area factor 2.3 m^2/ha) and percent canopy openness from hemispherical photographs by treatment and year, with standard error. Shaded bars are pre-fire treated areas.

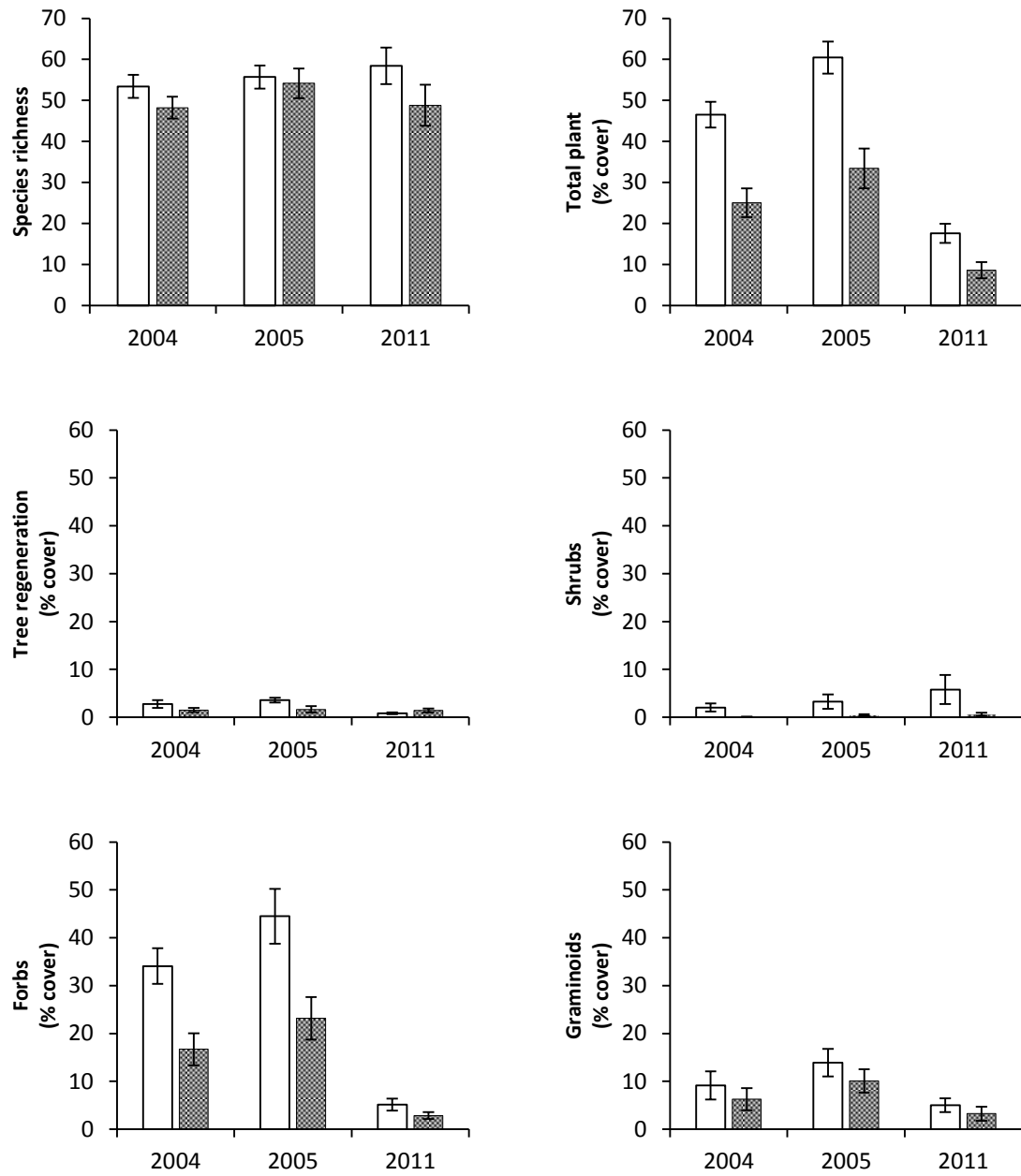


Figure 4. Total plant cover, species richness and cover by lifeform by treatment and year, with standard error. Shaded bars represent pre-fire treated areas.

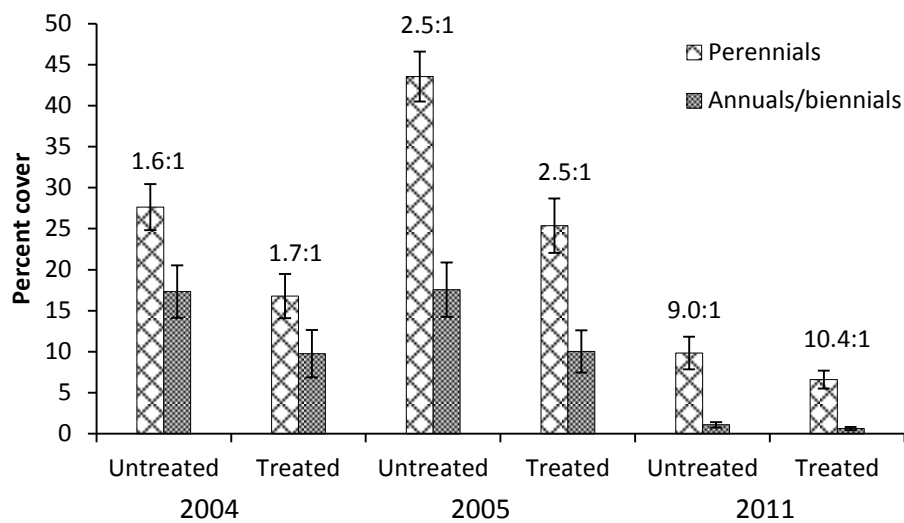


Figure 5. Cover of perennials and annuals/biennials by treatment and year with standard error. Perennial to annual/biennial ratios are above bars by pre-fire treatment for each year.

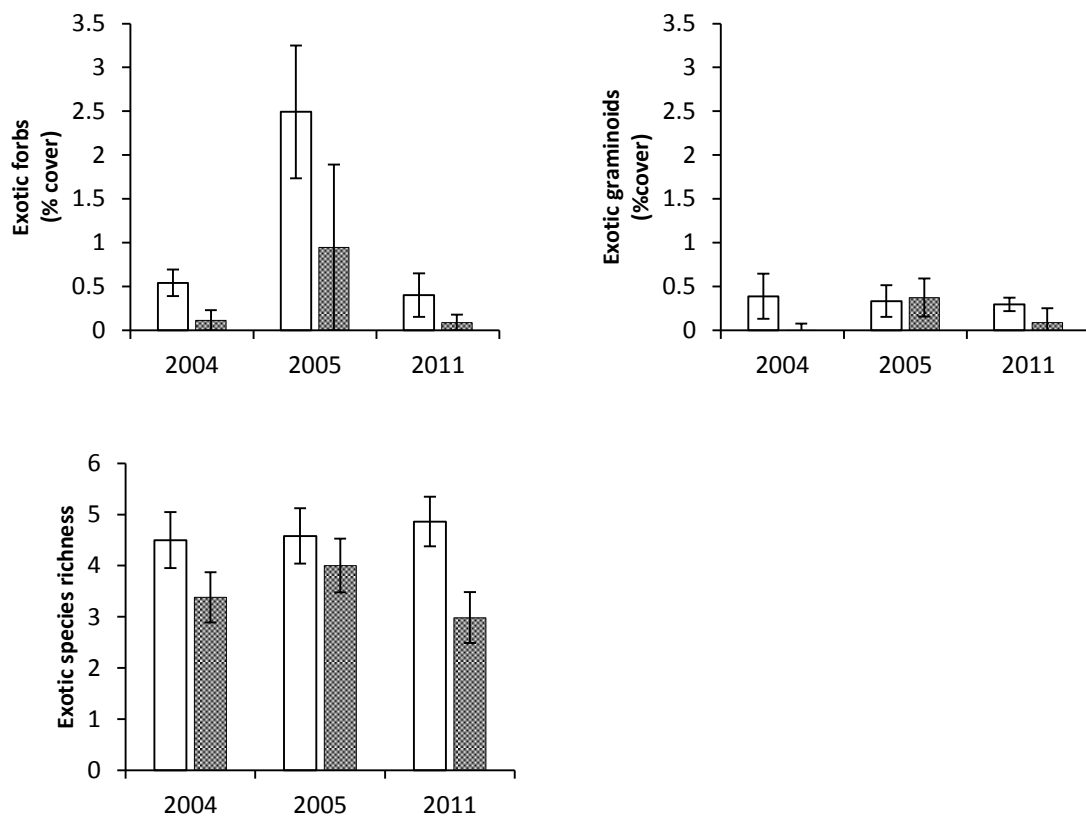


Figure 6. Cover of exotic forbs and graminoids as well as exotic species richness by treatment and year with standard error. Shaded bars represent pre-fire treated areas.

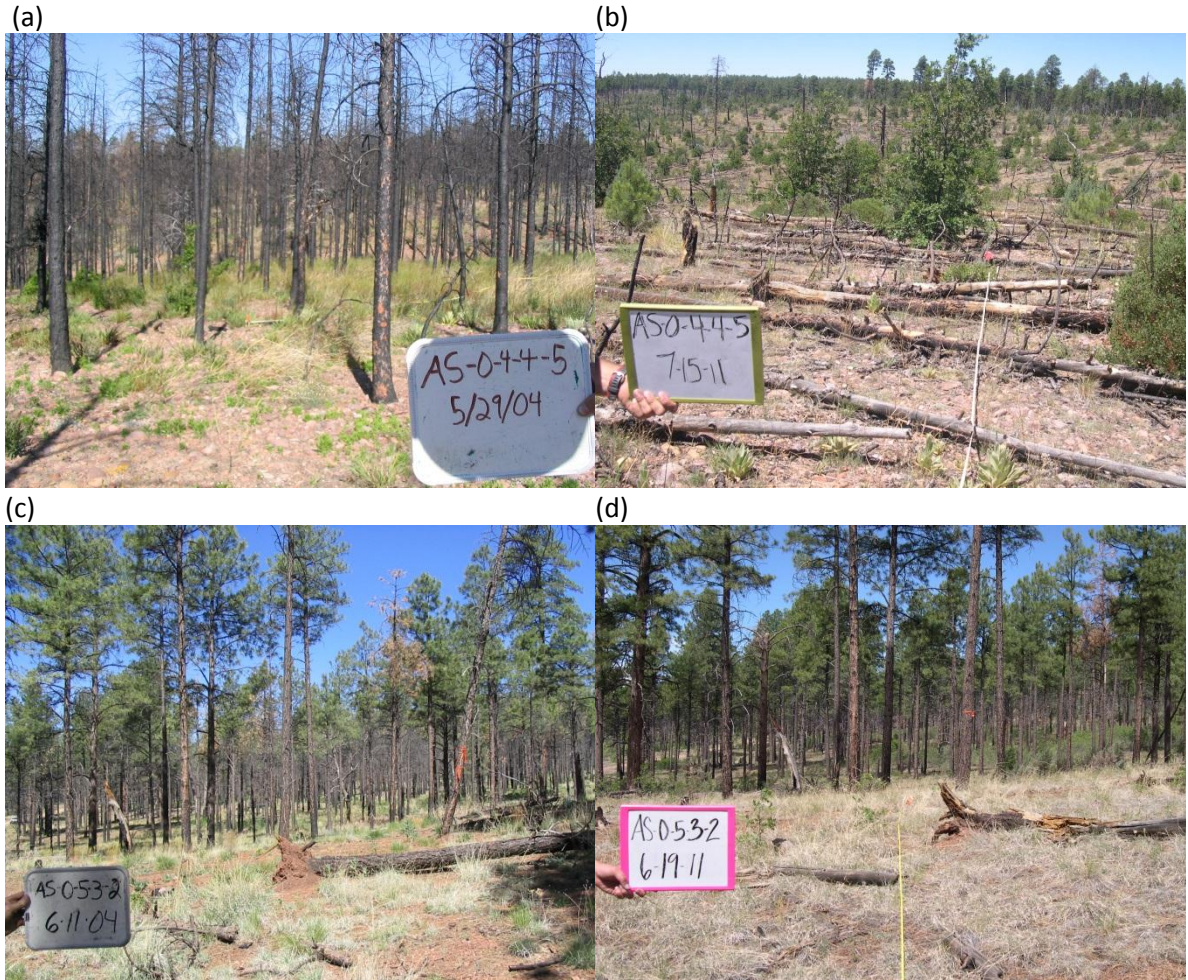


Figure 7. Photograph series of pre-fire untreated plot in 2004 (two years post-fire) (a), and 2011 (nine years post-fire) (b) above; below, pre-fire treated plot in 2004 (c) and 2011 (d).

CHAPTER 3

Pre-fire management treatments have lasting effects on post-fire plant community response

ABSTRACT

High severity fires in ponderosa pine forests of the Southwest have been increasing in frequency and extent. Severely burned areas have the potential to result in persistent type conversions to shrublands or grasslands, and they have also been associated with exotic species invasions. In response to the risk of high severity fire, land managers are routinely applying fuel reduction treatments to increase forest resilience, yet how these treatments may influence post-fire recovery in the longer-term is not well known. We re-measured existing plots on the 2002 Rodeo-Chediski Fire eight years after burning to detect longer-term trends in pine regeneration, as well as plant community and exotic species response. We compared high and low severity burned areas, and also examined how pre-fire treatment (cutting in an uneven-aged harvesting system with prescribed fire) modified vegetation response within severity class. We detected persistent differences between low and high severity areas, including significantly higher overall plant cover and shrub cover, and higher species richness on high severity areas. We also detected significantly higher exotic forb cover in high severity areas than in low severity areas, although overall exotic response was generally quite low (<1%). This represents a slight decrease in exotic cover since the initial 2004/2005 measurements; however, the frequency of several exotic species increased through time. On finer scales, pre-fire treatments modified several vegetation response variables that are ecologically important due to their influence on future reforestation in high severity areas. Where the burning conditions resulted in high severity fire in pre-fire treated areas, the overall patch size of high severity was reduced and resulted in a more heterogeneous mixture of low and moderate severity burning in the

neighborhood. This pattern decreased distance to seed source and was linked to higher frequency of pine regeneration. Fuels treatments are important because they reduce fire severity where applied. Our data provide additional support for conducting these treatments, because even where treated areas do burn severely, pre-fire treatments modify the heterogeneity of severity patterns to include more low and moderate severity areas in the neighborhood, which can influence forest regeneration.

INTRODUCTION

Severe large-scale fires, linked to uncharacteristically high fuels (Covington and Moore, 1994) and climate warming (Westerling *et al.*, 2006), have raised several important concerns about post-fire plant communities in the ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests of the Southwest, three of which we examine here. First, extensive forest areas that have burned severely may result in persistent conversions to shrublands or grasslands, rather than regenerate as forest (Savage and Mast, 2005), particularly under a warmer and drier climate (Seager *et al.*, 2007). The unprecedented size of high severity burned areas necessarily means that post-fire pine regeneration in these areas is not well understood, because it is occurring in relatively novel conditions. In addition, high severity fire may promote sprouting species over seeding species (such as ponderosa pine), because early site capture by sprouting species may limit seeder species establishment through competition for resources (Fulé and Covington, 1998; Barton, 2002). Furthermore, ponderosa pine can be considered a foundation species in these communities because it defines community structure by creating locally stable conditions for other species, and modulates fundamental ecosystem processes. The loss of a foundation species over large, landscape-scale areas can create novel species assemblages and degrade native habitats (Ellison *et al.*, 2005).

Exotic species invasions are another important concern since numerous studies have documented invasions following high severity fire events (Crawford *et al.*, 2001; Griffis *et al.*, 2001; Floyd *et al.*, 2006; Dodge *et al.*, 2008), which may not only impact native plant communities, but may also alter future fire regimes (Brooks *et al.*, 2004). Yet these invasions are not entirely predictable, since other high severity fire studies in the Southwest have documented a low exotic response (Foxy, 1996; Huisinga *et al.*, 2005; Kuenzi *et al.*, 2008). Lastly, the extent to which pre-fire treatments will influence post-fire successional pathways is of concerns as land managers are routinely applying fuel reduction treatments (thinning and/or burning) to increase forest resilience and reduce high severity fire risk (Baron *et al.*, 2009). These treatments generally reduce fire severity by reducing surface fuels, and reducing tree density and canopy connectivity (Pollet and Omi, 2002; Finney *et al.*, 2005; Strom and Fulé, 2007; Cochrane *et al.*, 2012; Fulé *et al.*, 2012), yet the influence of extreme fire weather conditions and topography can occasionally result in high severity fire in treated areas. Whether they burn under low or high severity, pre-fire treatments are likely to have long-term influences on post-fire recovery.

To investigate the longer-term effects of pre-wildfire treatments on pine regeneration and exotic response, we re-measured existing plots established after the 2002 Rodeo-Chediski Fire of northeastern Arizona (Strom, 2005; Kuenzi *et al.*, 2008). These plots were originally installed in 2004, when herbaceous understory, fuels, and forest structure response variables were measured in relation to fire severity and pre-fire treatment. Kuenzi *et al.* (2008) found that low and high severity areas had markedly different plant communities two and three years post-fire, which they primarily attributed to the near-complete loss of overstory trees in high severity areas (Kuenzi *et al.*, 2008). These early differences indicated two drastically different vegetation types on the landscape: (1) in the absence of another high severity fire event, the low severity

areas are likely to remain pine-dominated systems, whereas (2) high severity areas have the potential to convert to other vegetation types (Savage and Mast, 2005; Strom and Fulé, 2007; Haire and McGarigal, 2010). Our first hypothesis was that marked differences in plant communities between low and high severity areas would persist eight years post-fire (*Hypothesis 1: Low versus high severity fire areas*).

The 2004 data also show that low severity treated areas that were treated pre-fire had a more open structure (lower tree density and basal area, and higher canopy openness) than untreated low severity areas (Kuenzi *et al.*, 2008). We hypothesized that these trends in overstory structure variables would persist through 2010, leading to higher plant canopy cover, greater species richness, and higher frequencies of pine regeneration in relation to reduced tree canopy cover and a lower density of competing trees (*Hypothesis 2: Treatment effects in low severity areas*).

Third, the initial investigations documented that pre-fire treated areas had a lower percentage of high severity burning than untreated areas (Strom, 2005). We hypothesized that pre-fire treatment mitigated high severity fire and resulted in a more diverse mosaic of low and moderate severity in the “neighborhood” of our sampling sites. We then predicted that vegetation retention in low and moderate severity areas would provide both more seed sources and greater competition for resources in the neighborhood of treated sites, which would result in lower total plant cover, higher species richness and a higher relative frequency of pine regeneration (*Hypothesis 3: Treatment effects in high severity fire areas*).

We deliberately discuss some of the same response variables (pine regeneration relative frequency, plant foliar cover, etc.) in separate hypotheses because, as noted above, we predict some response variables will behave differently based on treatment within each severity class.

METHODS

Study area

The study area lies south of the Mogollon Rim in east-central Arizona on the White Mountain Apache Tribal (WMAT) lands. For the eight years of post-fire vegetation recovery, precipitation by water year has generally been below the 60-year average (Figure 1). The 60-year average by water year during this period was 45.0 cm, and total precipitation during 2010 was 35.2 cm. Average annual snowfall in the area was 102.4 cm, and there were 99.8 cm of snow over the winter of 2009/2010, which is only slightly below the 60-year average. The average maximum and minimum monthly temperatures were 29.2° C in July and -8.7° C in January. Weather data were recorded at the Heber Ranger Station by the Western Regional Climate Center (www.wrcc.dri.edu). This weather station is located above the Rim at an elevation of 1,984 m (16-311 m lower than the range of our study sites), approximately 12 km north of the study sites, on the edge of a ponderosa pine/pinyon-juniper transition zone and so may have recorded less precipitation and higher temperatures than our study sites experienced.

The study sites were selected in 2004, ranging in elevation from 2,000 to 2,295 m, on slopes <45% (average slope was 17.6%) (Strom, 2005; Kuenzi *et al.*, 2008). Study sites were stratified by severity classes (low and high), and by pre-fire management of (1) no treatment or (2) cut in an uneven-aged harvesting system and subsequently burned under prescription (hereafter: untreated, treated). Fire severity classes were determined by a combination of remotely sensed Differenced Normalized Burn Ratio (Δ NBR) maps and ground-truthing (Strom 2005). Pre-fire treatment areas were selected using treatment history data provided by the tribe and only included treatments conducted within 11 years prior to the Rodeo-Chediski Fire.

The high severity study areas were seeded immediately post-fire. The seed mix used on the WMAT lands included *Triticum aestivum* L. (common wheat), an exotic, but sterile, species

applied at a rate of 16.8 kg ha⁻¹. The remainder of the seed mix included species native to the region, but the seed source is unknown and therefore may not represent locally native genotypes: *Elymus trachycaulus* (Link) Gould ex Shinnars (slender wheatgrass), *Pascopyrum smithii* (Rydb.) A. Löve (western wheatgrass), *Panicum virgatum* L. (switchgrass), *Nassella viridula* (Trin.) Barkworth (green needlegrass), *Bromus marginatus* Nees ex Steud. (mountain brome) (*Bromus marginatus* = *Bromus carinatus* H. & A. (Welsh *et al.* 1993)), *Bouteloua curtipendula* (Michx.) Torr. (sideoats grama), *Sporobolus cryptandrus* (Torr.) Gray (sand dropseed), *Coreopsis tinctoria* Nutt. (plains coreopsis), *Dalea purpurea* Vent. (purple prairie clover), *Linum lewisii* Pursh (blue flax), and *Rudbeckia hirta* L. (black-eyed susan) (Kuenzi *et al.*, 2008).

Measurement

Six sites were originally installed within each of four treatment and severity combinations (total N = 24), with three subsample plots at each site. In 2010 we re-located 70 of the 72 original plots, such that two sites had only two subsample plots. All field protocols follow the original studies (Strom, 2005; Kuenzi *et al.*, 2008). We used a variable-radius prism plot (basal area factor 2.3 m²/ha) for overstory trees, on which we measured diameter at breast height (DBH, 1.37 m) and tree height. We tallied all pine regeneration shorter than breast height in a 3.1-m radius circle. Since smaller seedlings generally have high mortality rates (Smith *et al.*, 1997), we were interested in separating the more established seedlings from the very small seedlings, and so divided them into two height classes, 0-40 cm and 41-137 cm. We used a hemispherical fisheye lens (Nikon CoolPix E4300 and FC-E8 Fisheye Converter Lens) to photograph canopy cover, and then quantified canopy openness using the Gap Light Analyzer (Institute of Ecosystem Studies, 1999). In addition, we re-took the plot overview photos in order to create a photograph series through time.

We measured understory characteristics using two perpendicular 44.8-m transects to create the 1000-m² plot. Along each transect, we measured plant canopy cover from ten 20- X 50-cm quadrats, for a total of 20 quadrats per plot (Daubenmire, 1959). We recorded cover data by life form and nativity as well as by species, including trees shorter than 1.37 m, and recorded a species list for the entire plot area.

To directly compare our data, we followed Kuenzi *et al.*'s (2008) taxonomic and nativity classification which was based on the USDA-NRCS PLANTS database (USDA-NRCS, 2006). One exception they made was *Portulaca oleracea* L. (little hogweed), which was listed as "introduced" on the PLANTS database, but Kuenzi *et al.* (2008) classified it as "native" based on Byrne and McAndrews (1975). For species that were first detected in 2010, we used the more current USDA-NRCS PLANTS database (USDA-NRCS, 2011). When we were unable to identify plants to species, we classified them to the lowest taxonomic level we could identify with certainty, generally to the genus level.

To quantify neighborhood severity surrounding high severity sampling sites, we defined the potential seed contribution area for a site based on seed dispersal distances, which have been estimated at 1.5 times tree height (McDonald, 1980). Since there is some variability in the literature regarding the minimum seed tree size (Pearson, 1950; Larson and Schubert, 1970) we selected an intermediate DBH of those reported, 40.6 cm (16 in). We calculated the average height of trees this size or larger across our entire study area and calculated the estimated dispersal distance to be approximately 36 m. We then generated a buffer at least 36 m from any subsample plot at each study site, which resulted in an overall circular site buffer of 180 m from site center (Figure 2). Then we used the dNBR severity map to count the number of low, moderate and high severity pixels within the potential seed contribution area, and averaged

these by treatment. For consistency, all pixels that partially intersected the buffer were also included in the pixel counts.

Statistical Methods

For all analyses, we used site level means ($n = 24$). For Hypothesis 1 (*Low versus high severity*), we analyzed plant community data using a combination of univariate and multivariate statistical tests as well as ordination techniques. All plant community analyses were based on the subset of species that occurred in at least 5% of the plant cover quadrats, and richness analyses were based on species that occurred on at least 5% of the plot species lists, in order to reduce the influence of uncommon species (McCune and Grace, 2002). For overall plant community composition we used PC-ORD software (McCune and Mefford, 1999) to perform two-way PerMANOVA tests, a non-parametric permutation procedure, on burn severity (high, low) and pre-fire treatment (untreated, treated). We used the Bray-Curtis dissimilarity measure with 9999 permutations, with $\alpha = 0.05$. We analyzed differences among univariate response variables such as cover by life form and nativity, species richness and pine regeneration relative frequency with PerMANOVAs in PC-ORD, using Euclidean distance (Anderson, 2001).

To further examine our first hypothesis, that low and high severity areas remain distinct eight years post-fire, we graphically displayed community data in ordination space, using non-metric multidimensional scaling (NMDS). We conducted 250 runs with real data and 250 runs on randomizations from a random starting point, with an instability criterion of 0.00001. We chose the final number of axes based on stress levels <15 with p-values <0.05 (Peck, 2010). Finally, we also used PC-ORD to identify indicator species by severity, since the previous study documented that severity class had the strongest influence on the plant community (Kuenzi *et al.*, 2008). Indicator species analysis yields a value based on relative frequency and percent cover for each

species. Species with an indicator value > 25 and a p-value (based on a Monte Carlo test) of < 0.05 were considered indicator species for that severity class (Dufrene and Legendre, 1997).

We examined the same vegetation response variables in hypotheses two (*Treatment effects in low severity*) and three (*Treatment effects in high severity*) as we did for hypothesis one. However, since we were interested in treatment effects within severity class, here we first examined the interaction of treatment and severity. Where the interaction was significant ($\alpha = 0.05$) or approached significance, we tested treatment effects within severity class with a PerMANOVA and generated an NMDS ordination, both with the same parameters outlined above for the full model. We used a liberal definition of approaching significance because we were concerned about missing important differences by treatment within severity class, so we further explored any variable with an interaction p-value ≤ 0.20 .

Finally, to test for differences in neighborhood severity for hypothesis 3 (*Treatment effects in high severity*), we lumped the low and moderate severity pixel percentages, since both severity classes were considered proxies for seed sources. We then tested the differences in the proportion of low/moderate severity area between treated and untreated areas with a t test using JMP (JMP, Version 7).

RESULTS

We documented the presence of a total of 329 species from 190 genera and 60 families. For multivariate plant community analyses on cover we focused on the 104 species found on at least 5% of the cover quadrats, and for richness analyses we focused on the 172 species found on at least 5% of the plot census data. There was a total of 22 exotic species from 8 families, most from Poaceae (9) and Asteraceae (5); 10 of these were found on at least 5% of the plots (Table 1). The results below are presented as they relate to each hypothesis.

Hypothesis 1: Low versus High Severity Fire Areas

Low and high severity plant communities had significant differences in composition based on cover data by species ($p = 0.0001$). The NMDS ordination displays this distinction between low and high severity plant communities and how they align with differences in tree density, basal area and canopy openness, which are overlaid as vectors (Figure 3). PerMANOVA univariate tests for these vectors were all highly significant ($p = 0.0001$) between low and high severity areas, due to the loss of most overstory trees in high severity areas (Figure 4). These overstory structure drivers were linked with significantly higher total cover in high severity than low severity areas, a pattern reflected in the mean values for all life forms other than exotic graminoids. Shrub cover was a substantial component of the high severity area plant community, comprising nearly half of the mean total cover (Table 2, Figure 5). Additionally, the indicator species analysis included three shrub species for high severity areas: *Arctostaphylos pringlei* Parry (Pringle manzanita), *Arctostaphylos pungens* Kunth (pointleaf manzanita) and *Ceanothus fendleri* A. Gray (Fendler's ceanothus). Other indicator species for high severity included three native graminoid species seeded post-fire: *P. smithii*, *Panicum virgatum*, *B. curtipendula*. Notably, no indicator species were detected for low severity areas due to highly variable plant community composition.

Cover of exotic forbs was significantly higher ($p = 0.004$) in high severity areas but averaged <1% in both severities (0.66% in high severity areas and 0.008% in low severity areas). This difference was driven primarily by two species, *Tragopogon dubius* Scop. (yellow salsify) and *Verbascum thapsus* L. (common mullein), that were commonly found on high severity plots (32 of 35 plots and 30 of 35 plots, respectively). Although their overall cover values were low, the prevalence of these species is reflected in their designation as an indicator species of high severity areas (Table 3).

High severity areas also had significantly higher species richness than low severity areas ($p = 0.0071$). This was driven primarily by greater forb richness in high severity areas, where approximately 37 forb species were observed, versus 31 forb species in low severity areas. Pine regeneration density was highly variable. For the combined height classes, seedlings ha^{-1} ranged from 0 to 4283.2 in high severity areas and from 0 to 659.0 in low severity areas. In the 41-137 cm height class, density averaged 888.9 (S.E. 309.5) seedlings ha^{-1} in high severity areas and 13.73 (S.E. 13.73) seedlings ha^{-1} in low severity areas. To test our hypothesis, we focused on relative frequency of seedlings in the 41-137 cm height class, which were significantly more frequent ($p = 0.0056$) in high severity areas (0.51) compared to low severity areas (0.31) (Table 4).

Hypothesis 2: Treatment Effects in Low Severity Areas

None of the forest structure variables in low severity areas were significantly different between treated and untreated areas (Table 2). However, treated areas had lower mean tree density and basal area, and higher mean percent canopy openness (Figure 4). Significant differences were detected for plant community composition based on cover data by species between treated and untreated areas in low severity ($p = 0.047$). We attempted to generate an NMDS ordination and list of indicator species, but the data were too variable to detect patterns in either case.

Only forb cover was significantly higher in treated areas ($p = 0.039$), although mean cover values were higher in treated areas for all other metrics other than shrubs. Higher mean exotic graminoid cover in treated areas did approach significance ($p = 0.057$). This was driven primarily by one site with high cover values of *Eragrotis curvula* (Shrad.) Nees (weeping lovegrass), and several other sites with relatively high cover of *Poa pratensis* L. (Kentucky bluegrass).

Mean species richness was only slightly higher in treated areas (approximately 48 species versus 45 in untreated) and this difference was not significant ($p = 0.57$). Pine seedling density was extremely variable in the combined height classes, ranging from 82.4 to 659.0 seedlings ha^{-1} on treated sites versus 0 to 329.47 on untreated sites. In the 41-137 cm size class, there was an average of 123.6 (S.E. 84.4) in treated areas and 13.7 (S.E. 13.7) in untreated areas (Table 4). To test our hypothesis we focused on the average relative frequency of seedlings in the 41-137 cm height class, which was higher (0.17) in treated areas compared to untreated areas (0.06), although this difference was not significant ($p = 0.73$) (Table 4).

Hypothesis 3: Treatment Effects in High Severity Areas

The combined amount of low and moderate severity areas averaged 47.2% of the projected seed contribution area for untreated sites. This was significantly lower ($p = 0.03$) than the average of low and moderately burned areas (73.1%) at the treated high severity sites (Figure 6). Plant community composition based on cover data by species was significantly different between treated and untreated areas in high severity areas ($p = 0.01$), which is reflected in the NMDS ordination (Figure 7). Total cover was significantly higher in untreated areas ($p = 0.03$). The cover of other life forms did not differ significantly by treatment, although the means for all were higher in untreated areas as predicted (Table 2, Figure 5). Exotic forb and exotic graminoid cover also followed this trend, but the differences in means were $< 0.07\%$ and the standard errors were greater than their means, indicating exceptionally high variability.

There was no significant difference in plant species richness between high severity treated and untreated areas, although mean richness was slightly higher in treated areas (approximately 59 species) versus untreated areas (approximately 53 species) (Table 2, Figure 5). Pine seedling density in the combined height classes on treated sites ranged from 164.7 to 4283.2 seedlings ha^{-1} versus 0 to 2347.5 seedlings ha^{-1} on untreated sites. In the 41-137 cm size

class, there was an average of 1345.4 (S.E. 435.7) seedlings ha⁻¹ in treated areas and 432.44 (S.E. 385.1) in untreated areas (Table 4). To test our hypothesis, we focused on relative pine regeneration frequency in the 41-137 cm height class, and found significantly more frequent pine regeneration in treated areas (0.67) than untreated areas (0.19) ($p = 0.027$) (Tables 2, 4).

DISCUSSION

Hypothesis 1: Low versus High Severity Areas

Our hypothesis that fire severity had a persistent impact on post-fire vegetation characteristics eight years post-fire was upheld. We observed large and significant differences between low and high severity areas for almost all variables measured. In high severity areas, the resources made available after the loss of mature trees likely enabled higher understory plant canopy cover, of which nearly half was comprised of shrubs. The combination of few to no overstory trees and high shrub cover has resulted in shrub-dominated communities, unlike low severity areas where mature ponderosa pine dominance was maintained post-fire.

These distinct high severity fire areas are of particular concern in part because high severity fires have been implicated in exotic species invasions in the ponderosa pine forests of the Southwest (Crawford *et al.*, 2001; Griffis *et al.*, 2001; Barclay *et al.*, 2004; Dodge *et al.*, 2008). We found very low cover of exotic species overall, similar to findings by Huisinga *et al.* (2005) on the North Rim of the Grand Canyon and Foxx (1996) in northern New Mexico. Our 2010 overall exotic cover value for all severity/treatment combinations was <2%, which is slightly lower than the <3% observed in 2004 and 2005 (Kuenzi *et al.*, 2008), yet this difference is certainly within the range of potential observer differences. Drought conditions for the period of recovery may be contributing to the overall low exotic response, and low propagule pressure may also play a role (Lockwood *et al.*, 2005).

In addition to low exotic cover, we found slightly lower exotic species richness than that reported in the initial investigation by Kuenzi *et al.* (2008). We observed a total of 23 exotic species, 11 of which were on at least 5% of the plots, whereas Kuenzi *et al.* (2008) observed 35 species overall and 13 that occurred on at least 5% of the plots. Of the exotic species found on at least 5% of the plots, five species observed in 2004 and 2005 were not included on the 5% subset list in 2010: *Agropyron desertorum* (Fisch. ex Link) Schult. (desert wheatgrass), *Dactylis gomerata* L. (orchardgrass), *T. aestivum*, *Cirsium vulgare* (Savi) Ten. (bull thistle), and *Chenopodium album* L. (lambsquarters). Our lack of detection of *C. album* may not represent an actual change, since the *Chenopodium* plants we encountered were in a juvenile stage that did not allow us to distinguish between native and exotic *Chenopodium* species. The common wheat seeded immediately post-fire was frequent in 2004, infrequent in 2005 (Kuenzi *et al.* 2008), and entirely absent in 2010. Our data show that the annual cereal grain did quickly exit the system as intended by managers (Peppin *et al.*, 2010). The remaining three exotic species from the 2004/2005 observations were still observed in 2010, but they occurred on less than 5% of the plots. In addition, four exotic species that were observed infrequently in 2004/2005 were detected on at least 5% of plots in 2010: *E. curvula*, *Poa compressa* L. (Canada bluegrass), *P. pratensis*, and *Erodium cicutarium* (L.) L'Hér. ex Aiton (redstem stork's bill). Only the perennial forb, *Sanguisorba minor* Scop. (small burnet), was completely new in 2010, yet it occurred on only two plots. The perennial grass *E. curvula* was seeded in the course of past management activities before the Rodeo-Chediski Fire (Kuenzi *et al.* 2008). Many of the other exotic species we found are known to have been seeded as part of management activities throughout the Southwest: *P. pratensis*, *S. minor*, *Melilotus officinalis* (L.) Lam. (sweetclover), *D. glomerata* (Fowler *et al.*, 2008; Wolfson and Sieg, in prep). Also, seed mixes can be contaminated with

exotic species, so past seeding practices in the area may have introduced some of the exotics we detected (Keeley, 2006; Fowler *et al.*, 2008; Peppin *et al.*, 2010).

In contrast to earlier measurements, exotic forb cover was significantly higher in high severity fire areas, although it was still quite low at <1%. This difference was driven by the prevalence of two exotic forbs, *T. dubius* and *V. thapsus*. Although cover values for each were relatively low, the number of plots with these species steadily increased since the initial investigation in 2004, particularly for *T. dubius*. This species was found on 51.4% more high severity plots in 2010 than in 2004, and *V. thapsus* was found on 11.4% more high severity plots. This pattern is further reflected in by the designation of both species as indicator species for high severity in 2010, which was not the case in 2004 or 2005. The increase of *V. thapsus* through time in cover and frequency among plots was also observed on the Apache-Sitgreaves National Forest portion of this fire (discussed in Chapter 2), but is in contrast to the reductions detected elsewhere on the Rodeo-Chediski Fire. Ffolliot *et al.* (2011) found reductions in *V. thapsus* by five years post-fire, which is consistent with the reductions observed by Stoddard *et al.* (2010) after low severity restoration treatments. On our sites, the current prevalence of either *T. dubius* or *V. thapsus* may become cause for concern in the future if it enables widespread buildup of sufficient propagule pressure that could facilitate more significant invasions (Lockwood *et al.*, 2005; Moles *et al.*, 2012).

Tracking these exotic species on high severity fires through time is important for management and for our understanding of invasion patterns, since the prevalent notion that high severity fire results in exotic species invasions is not always the case. Not only have several studies documented a low exotic response, but our ability to compare our data with other studies is limited because several studies that documented heavier invasions in the Southwest did not explicitly state which exotic species were observed (Griffis *et al.*, 2001) and some used

different definitions of species' nativity (Crawford *et al.*, 2001; Barclay *et al.*, 2004). Finally, the degree to which exotic species invasions are facilitated by disturbance has been called into question. A recent review by Moles *et al.* (2012) found that changes to disturbance regimes in a given ecosystem explained nearly twice as much variation in invasion events than historical disturbance regimes, but that the total variation explained by any sort of disturbance was <7%. Although we did find higher exotic cover in the high severity areas that would represent the changed disturbance regime, this difference was small, making the link with a changed disturbance regime unclear on our sites.

Hypothesis 2: Treatment Effects in Low Severity Areas

Our hypothesis that forest structure was more open in pre-fire treated areas than untreated areas within low severity was not upheld, so it is not surprising that the subsequent predictions about the effects of a more open structure were also generally not upheld. However, although not significantly different, trends in mean tree density, basal area, and canopy openness did indicate a more open structure. In turn, mean understory response was more abundant as expected, similar to what has been reported in previous studies (Moore and Deiter, 1992; Moore *et al.*, 2006).

Finally, although also not significant, the higher frequency of pine regeneration in low severity treated areas versus low severity untreated areas may be important for concerns about seedling recruitment in post-settlement forests. In addition to reducing forest fire risk, thinning and burning treatments are also applied to promote recruitment of the next cohort of the shade-intolerant ponderosa pine. We detected no significant differences in relative frequency of regeneration in the 41-137 cm height class ("established" seedlings). However, when both classes were combined, the mean relative frequency was higher in treated areas, where every

site had regeneration on at least one plot. In contrast, four of the six untreated low severity sites completely lacked ponderosa pine regeneration.

The pine regeneration densities we detected are difficult to compare directly to other studies due to differences in the definition of seedling size and so we report them along with their seedling definitions. Studies on the 2000 Jasper Fire in the Black Hills observed ponderosa pine regeneration densities up to 2,000 seedlings ha⁻¹ five years post-fire (Keyser *et al.*, 2008), and 612 seedlings ha⁻¹ three years post-fire (Lentile *et al.*, 2005) in low severity burned areas. Both studies defined seedlings as <1.4 m tall, which is most similar to our definition. In the Southwest, Puhlick *et al.* (2012) observed 536-14,184 seedlings ha⁻¹, but defined seedlings as ≥20 cm in height and < 2.54 cm DBH, considerably larger than our upper limit. Bailey and Covington (2002) examined regeneration in thinned as well as in thinned and burned stands and found much lower rates of regeneration, from 18-60 seedlings ha⁻¹ in two study areas. These numbers are considerably lower than we observed, despite their more inclusive definition (≥ 20 cm in height, ≤ 5 cm DBH). In contrast to these studies, we detected an average of 96 seedlings ha⁻¹ in untreated low severity areas and 288 seedlings ha⁻¹ in treated low severity areas, for both classes combined. Although these numbers are higher than Bailey and Covington's (2002), they are much lower than other studies included here. However, a historical ecology study by Mast *et al.* (1999) near Flagstaff, AZ determined that ponderosa pine trees recruited into the overstory at a rate of 0.4-3.6 trees ha⁻¹, per decade under the pre-European fire regime. Although significant mortality is likely, our seedling densities may be adequate to provide for future recruitment into the overstory in the treated areas (Mast *et al.*, 1999).

Hypothesis 3: Treatment Effects in High Severity Areas

Our hypothesis that treated high severity areas would have more low and moderate severity in proximity of our sampling sites was upheld. Our related hypothesis that this would

result in lower overall plant cover, and higher plant species richness and relative frequency of pine regeneration, was also predominantly upheld. There was significantly lower total cover and higher relative frequency of pine regeneration in treated areas, and the remaining variable mean responses were as predicted (although not significant). On the basis of relative frequency of pine regeneration, which likely best reflects broader landscape patterns, our data indicate that untreated areas are more likely to remain shrub-dominated, whereas treated areas have a better chance of recruitment back to pine-dominated forest.

Relative frequency is a good reflection of pine regeneration across the landscape, but density estimates may provide insights on localized patterns. Specifically, two of the treated sites had relatively high pine seedling densities, which may indicate a trajectory towards dog-hair thickets. The densities at these sites (>2000 seedlings ha^{-1}) greatly exceed the ~ 809 seedlings ha^{-1} Pearson (1950) recommended to fully re-stock clearcut areas. These numbers are well beyond those required for current goals of uneven-aged stands with historical structures (although we note that Pearson does not specify size class in this recommendation). Similarly high densities have also been reported in two longer-term investigations. Savage and Mast (2005) examined ten high severity fires 24-53 years post-fire and found exceptionally dense ponderosa pine stands in four sites. In order to directly compare our data with Savage and Mast's (2005), which is reported by adult, sapling and seedling densities, we summed these three categories for a total of 1,597 to 7,912 stems ha^{-1} (however, two of these sites had minor tree planting post-fire). Finally, Haire and McGarigal (2010) also reported relatively high densities on two fires that burned 28 and 45 years prior: 8,000 and 2,000 ha^{-1} , respectively. They defined pine regeneration was defined via quantification of tree ages and included any trees that established in the post-fire years (Haire and McGarigal, 2010). These studies suggest that

without management intervention, our high-density high severity treated sites are likely to remain dense doghair thickets, and therefore at risk of high severity re-burning in the future.

Both the frequency and density measures of seedlings on untreated high severity sites indicate a high likelihood of conversion to shrublands. In the larger 41-137 cm size class, only two of six sites had any ponderosa pine regeneration. For both sizes combined, regeneration occurred on three of six sites, averaging 446 seedlings ha⁻¹ for both size classes (14 of which were in the 0-40 cm class). Two of the three sites had densities < 250 seedlings ha⁻¹. Since these areas are devoid of overstory trees, these numbers may be too low to regenerate a forested landscape in the near future. This number is slightly higher than those reported in several other studies in the ponderosa pine type. On the La Mesa Fire in northern New Mexico, Foxx (1994) reported roughly 81-121 seedlings ha⁻¹; whereas in high severity areas of the 2000 Jasper Fire in the Black Hills, no seedlings were detected in severely burned areas in either year five post-fire (Keyser *et al.*, 2008) or year three post-fire (Lentile *et al.*, 2005).

We attribute the low relative frequency and density of pine recruitment in our high severity untreated sites in part to distance to seed source and early site-capture by shrubs and sprouting species. Other studies in ponderosa pine have shown decreased recruitment with increasing distance from unburned, or lightly burned, edge (Bonnet *et al.*, 2005; Lentile *et al.*, 2005; Haire and McGarigal, 2008, 2010). Like other studies of high severity fire in ponderosa pine, we observed lower rates of recruitment in areas farther from lesser-burned edges (in our study, the proxy for this was the low and moderate severity areas that were less prevalent around the untreated sites). By increasing high severity patch size, these recent “mega-fires” are increasing the distance to edge/seed source, which may impact future forest regeneration, particularly given predictions of warmer and drier conditions in the future (Seager *et al.*, 2007).

However, it is important to note that patterns of both burning and regeneration are complex processes that are not entirely predictable, and all high severity patches may not face the same limitations. Several studies in historically frequent-fire systems have noted the difficulties in modeling post-fire long-distance seed dispersal, which may be important for long-term recruitment patterns by minimizing distance to seed source in the interior of high severity patches (Bonnet *et al.*, 2005; Haire and McGarigal, 2010). Similarly, some overstory trees occasionally survive within a high severity patch, which may act to reduce the effective patch size in terms of distance to seed source.

In addition to recruitment limitations due to distance to seed source, site capture by shrubs or grasses may inhibit future regeneration. Several studies have linked increased shrub cover to decreased pine regeneration (Strom and Fulé, 2007; Haire and McGarigal, 2008, 2010). We observed significantly higher total plant canopy cover on untreated high severity sites, where regeneration was lower. Means by life form suggest this is primarily driven by trees, shrubs and graminoids. We note that we used the same protocols to define “tree” species as the initial study but observed that much of the cover of “trees” under breast height is from sprouting species that are considered trees as adults but have a shrub-like habit during early growth stages (such as *Quercus gambelii* Nutt. (Gambel oak), *Juniperus deppeana* Steud. (alligator juniper) and *Robinia neomexicana* A. Gray (New Mexico locust)). These values then may be more complementary than distinct from the shrub cover values. Additionally, trees above breast height were not measured in the cover quadrats because they were intended to be sampled in the variable radius prism plots. However, these plots often will not include the extremely small diameter leaders of these young trees that are growing into the overstory. In that sense, our measurements may have underestimated the strength of this early site capture by sprouting species on our sites.

CONCLUSIONS

Not only did we detect important, persistent differences in vegetation response by severity, we also found important differences by pre-fire treatment within severity class. This demonstrates that landscapes that burned under a given severity class are not necessarily alike. As such, managing post-fire landscapes under the assumptions that all low or high severity areas are the same may ignore important differences in plant communities, exotic response and future trajectories.

Given the likelihood of more intense and severe fires in the future, concerns about exotic species invasions and future reforestation are mounting. Our data fit into a body of literature that does not indicate a straightforward or easily predictable pattern of exotic response, suggesting more intensive investigations are needed. Where existing plots burn over on public lands, managers and scientists should make re-measurements a priority in order to better understand how pre-fire species assemblages interact with severity and management treatments to influence post-fire plant communities and exotic response.

Re-measurements into the future, beyond the first few years post-fire, will be necessary to better understand future successional trajectories. Although future forest regeneration is not always predictable, our data are supported by other studies that show treatments such as thinning and burning are important to the persistence of ponderosa pine forests for two reasons. First, these treatments generally reduce fire severity and therefore retain the foundation tree species post-fire. Second, even where burning conditions permit high severity fire in treated areas, patch size is likely to be small, which may significantly impact post-fire trajectories through increased rates of pine regeneration.

REFERENCES

- Anderson, M.J., 2001. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 626-639.
- Bailey, J.D., Covington, W.W., 2002. Evaluating ponderosa pine regeneration rates following ecological restoration treatments in northern Arizona, USA. *Forest Ecology and Management* 155, 271-278.
- Barclay, A.D., Betancourt, J.L., Allen, C.D., 2004. Effects of seeding ryegrass (*Lolium multiflorum*) on vegetation recovery following fire in a ponderosa pine (*Pinus ponderosa*) forest. *International Journal of Wildland Fire* 13, 183-194.
- Baron, J.S., Gunderson, L., Allen, C.D., Fleishman, E., McKenzie, D., Meyerson, L.A., Oropeza, J., Stephenson, N., 2009. Options for National Parks and Reserves for Adapting to Climate Change. *Environmental Management* 44, 1033-1042.
- Barton, A.M., 2002. Intense wildfire in southeastern Arizona: transformation of a Madrean oak-pine forest to oak woodland. *Forest Ecology and Management* 165, 205-212.
- Bonnet, V.H., Schoettle, A.W., Shepperd, W.D., 2005. Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 35, 37-47.
- Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677-688.
- Byrne, R., McAndrews, J.H., 1975. Pre-Columbian Purslane (*Portulaca-Oleracea* L) in New World. *Nature* 253, 726-727.
- Cochrane, M.A., Morgan, C.J., Wimberly, M.C., Baer, A.D., Finney, M.A., Beckendorf, K.L., Eidenshink, J., Zhu, Z., 2012. Estimation of wildfire size and risk changes due to fuel treatments. *International Journal of Wildland Fire* Open access: <http://dx.doi.org/10.1071/WF11079>.
- Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa forest structure - changes since Euro-American settlement. *Journal of Forestry* 92, 39-47.
- Crawford, J.S., Wahren, C.H.A., Kyle, S., Moir, W.H., 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *Journal of Vegetation Science* 12, 261-268.
- Daubenmire, R.F., 1959. A canopy-coverage method. *Northwest Science* 33, 43-64.
- Dodge, R.S., Fulé, P.Z., Sieg, C.H., 2008. Dalmatian toadflax (*Linaria dalmatica*) response to wildfire in a southwestern USA forest. *Ecoscience* 15, 213-222.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67, 345-366.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3, 479-486.

Ffolliott, P.F., Stropki, C.L., Chen, H., Neary, D.G., 2011. The 2002 Rodeo-Chediski Wildfire's Impacts on Southwestern Ponderosa Pine Ecosystems, Hydrology and Fuels. United States Department of Agriculture / Forest Service Research Paper RMRS-RP-85.

Finney, M.A., McHugh, C.W., Grenfell, I.C., 2005. Stand- and landscape-level effects of prescribed burning on two Arizona wildfires. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 35, 1714-1722.

Floyd, M.L., Hanna, D., Romme, W.H., Crews, T.E., 2006. Predicting and mitigating weed invasions to restore natural post-fire succession in Mesa Verde National Park, Colorado, USA. *International Journal of Wildland Fire* 15, 247-259.

Fowler, J.F., Sieg, C.H., Dickson, B.G., Saab, V., 2008. Exotic plant species diversity: Influence of roads and prescribed fire in Arizona ponderosa pine forests. *Rangeland Ecology & Management* 61, 284-293.

Fox, T.S., 1996. Vegetation succession after the La Mesa fire at Bandelier National Monument. In: Allen, C.D. (Ed.), *Fire Effects in Southwestern Forests: Proceedings of the Second La Mesa Fire Symposium*, 29-31 March 1994. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, Los Alamos, NM, pp. 47-69.

Fulé, P.Z., Covington, W.W., 1998. Spatial patterns of Mexican pine-oak forests under different recent fire regimes. *Plant Ecol.* 134, 197-209.

Fulé, P.Z., Crouse, J.E., Roccaforte, J.P., Kalies, E.L., 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *Forest Ecology and Management* 269, 68-81.

Griffis, K.L., Crawford, J.A., Wagner, M.R., Moir, W.H., 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. *Forest Ecology and Management* 146, 239-245.

Haire, S.L., McGarigal, K., 2008. Inhabitants of landscape scars: Succession of woody plants after large, severe forest fires in Arizona and New Mexico. *Southwestern Naturalist* 53, 146-161.

Haire, S.L., McGarigal, K., 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. *Landscape Ecology* 25, 1055-1069.

Huisinga, K.D., Laughlin, D.C., Fulé, P.Z., Springer, J.D., McGlone, C.M., 2005. Effects of an intense prescribed fire on understory vegetation in a mixed conifer forest. *Journal of the Torrey Botanical Society* 132, 590-601.

Institute of Ecosystem Studies, 1999. Gap Light Analyzer (Computer Program). Simon Fraser University <http://www.ecostudies.org/gla>.

JMP, Version 7. SAS Institute Inc. In, Cary, NC, 1989-2007.

Keeley, J.E., 2006. Fire management impacts on invasive plants in the western United States. *Conservation Biology* 20, 375-384.

Keyser, T.L., Lentile, L.B., Smith, F.W., Shepperd, W.D., 2008. Changes in forest structure after a large, mixed-severity wildfire in ponderosa pine forests of the Black Hills, South Dakota, USA. *Forest Science* 54, 328-338.

Kuenzi, A.M., Fulé, P.Z., Sieg, C.H., 2008. Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. *Forest Ecology and Management* 255, 855-865.

Larson, M.M., Schubert, G.H., 1970. Cone crops of ponderosa pine in central Arizona including the influence of Albert squirrels. USDA Forest Service Research Paper RM-58.

Lentile, L.B., Smith, F.W., Shepperd, W.D., 2005. Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 35, 2875-2885.

Lockwood, J.L., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution* 20, 223-228.

Mast, J.N., Fulé, P.Z., Moore, M.M., Covington, W.W., Waltz, A.E.M., 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. *Ecological Applications* 9, 228-239.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., Mefford, M.J., 1999. PC-ORD (Computer Software). Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, OR.

McDonald, P.M., 1980. Seed dissemination in small clearcuttings in north-central California. USDA Forest Service Research Paper PSW-150, 5.

Moles, A.T., Flores-Moreno, H., Bonser, S.P., Warton, D.I., Helm, A., Warman, L., Eldridge, D.J., Jurado, E., Hemmings, F.A., Reich, P.B., Cavender-Bares, J., Seabloom, E.W., Mayfield, M.M., Sheil, D., Djietror, J.C., Peri, P.L., Enrico, L., Cabido, M.R., Setterfield, S.A., Lehmann, C.E.R., Thomson, F.J., 2012. Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology* 100, 116-127.

- Moore, M.M., Casey, C.A., Bakker, J.D., Springer, J.D., Fulé, P.Z., Covington, W.W., Laughlin, D.C., 2006. Herbaceous vegetation responses (1992-2004) to restoration treatments in a Ponderosa pine forest. *Rangeland Ecology & Management* 59, 135-144.
- Moore, M.M., Deiter, D.A., 1992. Stand density index as a predictor of forage production in northern Arizona pine forest. *Journal of Range Management* 45, 267-271.
- Pearson, G.A., 1950. Management of Ponderosa Pine the Southwest. United States Forest Service Agricultural Monograph 6, 217.
- Peck, J.E., 2010. Multivariate Analysis for Community Ecologists: Step-by-Step using PC-ORD. MjM Software Design, Gleneden Beach, OR.
- Peppin, D., Fule, P.Z., Sieg, C.H., Beyers, J.L., Hunter, M.E., 2010. Post-wildfire seeding in forests of the western United States: An evidence-based review. *Forest Ecology and Management* 260, 573-586.
- Pollet, J., Omi, P.N., 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *International Journal of Wildland Fire* 11, 1-10.
- Puhlick, J.J., Laughlin, D.C., Moore, M.M., 2012. Factors influencing ponderosa pine regeneration in the southwestern USA. *Forest Ecology and Management* 264, 10-19.
- Savage, M., Mast, J.N., 2005. How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 35, 967-977.
- Seager, R., Ting, M.F., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.P., Harnik, N., Leetmaa, A., Lau, N.C., Li, C.H., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316, 1181-1184.
- Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. The Practice of Silviculture: Applied Forest Ecology. John Wiley & Sons, New York.
- Stoddard, M.T., McGlone, C.M., Fulé, P.Z., Laughlin, D.C., Daniels, M.L., 2011. Native plants dominate understory vegetation following ponderosa pine forest restoration treatments. *Western North American Naturalist* 71, 206-214.
- Strom, B.A., 2005. Pre-fire treatment effects and post-fire forest dynamics on the Rodeo-Chediski burn area, Arizona. M.S. Thesis, School of Forestry, Flagstaff AZ, Northern Arizona University.
- Strom, B.A., Fulé, P.Z., 2007. Pre-wildfire fuel treatments affect long-term ponderosa pine forest dynamics. *International Journal of Wildland Fire* 16, 128-138.
- USDA-NRCS, 2006. The PLANTS Database (<http://plants.usda.gov>, 29 November 2006). National Plant Data Center, Baton Rouge, LA 70874-4490, USA.

USDA-NRCS, 2011. The PLANTS Database (<http://plants.usda.gov>, 15 November 2011). National Plant Data Center, Baton Rouge, LA 70874-4490, USA.

Welsh, S.L., Atwood, N.D., Goodrich, S., Higgins, L.C., 1993. A Utah Flora. Brigham Young University, Provo, UT.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940-943.

Wolfson, B.A.S., Sieg, C.H., In prep. 40-year post fire seeding trends in Arizona and New Mexico. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Table 1. Exotic graminoid and forb species by severity class. Seeded species include species known to have been seeded on the WMAT lands, not necessarily after the Rodeo-Chediski Fire (Kuenzi et al. 2008). Bolded species were found on at least 5% of plots.

Graminoids		
Severity	Seeded	Other
High	<i>Agropyron desertorum</i> ^a	<i>Bromus japonicus</i> ^a
	<i>Dactylis glomerata</i> ^a	<i>Bromus tectorum</i> ^a
	<i>Eragrostis curvula</i> ^a	<i>Echinochloa crus-galli</i>
		<i>Poa compressa</i>
		<i>Poa pratensis</i> ^a
		<i>Setaria viridis</i>
Low	<i>Dactylis glomerata</i> ^a	<i>Bromus tectorum</i> ^a
	<i>Eragrostis curvula</i> ^a	<i>Poa compressa</i>
		<i>Poa pratensis</i> ^a
Forbs		
Severity	Seeded	Other
High	none	<i>Cirsium vulgare</i> ^a
		<i>Erodium cicutarium</i> ^a
		<i>Lactuca serriola</i> ^a
		<i>Malva neglecta</i>
		<i>Medicago lupulina</i> ^a
		<i>Melilotus officinalis</i> ^a
		<i>Onopordum acanthium</i>
		<i>Polygonum aviculare</i> ^b
		<i>Rumex acetosella</i>
		<i>Taraxacum officinale</i>
		<i>Tragopogon dubius</i>
		<i>Verbascum thapsus</i>
Low	none	<i>Cirsium vulgare</i> ^a
		<i>Erodium cicutarium</i> ^a
		<i>Lactuca serriola</i> ^a
		<i>Medicago lupulina</i> ^a
		<i>Melilotus officinalis</i> ^a
		<i>Rumex acetosella</i>
		<i>Rumex crispus</i>
		<i>Sanguisorba minor</i>
		<i>Verbascum thapsus</i>

^a Species that have been seeded as part of management practices in the Southwest (Fowler *et al.*, 2008; Wolfson and Sieg, in prep).

Table 2. Results of perMANOVA tests for differences in univariate response variables. Significance is denoted by bold type and asterisk. Where the p-value for the interaction was significant or approached significance, we separated the data by severity to test for treatment effects.

Response variable	Severity	Treatment	Interaction	Treatment in High Severity	Treatment in Low Severity
Overstory tree density	0.0001*	0.40	0.34	NA*	
Basal area	0.0001*	0.14	0.059	NA*	0.12
Canopy openness	0.0001*	0.14	0.39	NA*	0.42
Total plant cover	0.0001*	0.02*	0.019*	0.033*	0.25
Tree regeneration	0.0045*	0.45	0.03*	0.12	0.067
Shrub cover	0.0001*	0.07*	0.32		
Forb cover	0.0015*	0.45	0.075	0.49	0.039*
Graminoid cover	0.0081*	0.57	0.14	0.3416	0.1853
Exotic forb cover	0.0040*	0.97	0.91		
Exotic graminoid cover	0.65	0.23	0.16	0.95	0.057
Total plant species	0.0071*	0.20	0.63		
Exotic species richness	0.07	0.36	0.14	0.6313	0.1818
Native species	0.10	0.61	0.33		
Pine regeneration (40-137 cm) frequency	0.0056*	0.0081*	0.079	0.027*	0.73

**We did not test overstory variables for treatment effects in high severity since they were not relevant to our hypotheses.*

Table 3. High severity indicator species. No indicator species were found for low severity. Exotic species are in bold.

Species	Indicator Value (IV)	p-value	Mean Cover	S.E.
<i>Arctostaphylos pringlei</i>	46.7	0.036	2.87	0.83
<i>Arctostaphylos pungens</i>	55.6	0.032	3.29	0.95
<i>Bouteloua curtipendula</i> ^a	73.1	0.004	1.55	0.45
<i>Carex sp.</i>	65.3	0.024	1.03	0.30
<i>Ceanothus fendleri</i>	79.7	0.004	14.25	4.11
<i>Cirsium wheeleri</i>	84.5	0.004	0.81	0.23
<i>Dyssodia papposa</i>	41.7	0.036	0.06	0.017
<i>Lotus wrightii</i>	87.9	0.004	0.55	0.16
<i>Panicum virgatum</i>	41.7	0.048	0.30	0.09
<i>Pascopyrum smithii</i> ^a	74.9	0.004	3.20	0.92
<i>Robinia neomexicana</i>	65.6	0.004	4.25	1.23
<i>Tragopogon dubius</i> ^b	75.0	0.004	0.05	0.016
<i>Verbascum thapsus</i> ^b	73.8	0.016	0.55	0.16

^aseeded; ^bexotic

Table 4. Pine regeneration mean relative frequency and mean density (standard errors are in parentheses). Presented by severity and treatment, in the 0-40 cm and 41-137 cm height classes, as well as the two classes combined ("All seedlings").

Severity/ Treatment	Relative frequency			Density (seedlings ha⁻¹)		
	0-40 cm	41-137 cm	All seedlings	0-40 cm	41-137 cm	All seedlings
Low						
Untreated	0.17(0.11)	0.06(0.06)	0.17(0.14)	82.4(56.3)	13.7(13.7)	96.1(61.7)
Treated	0.39(0.06)	0.17(0.11)	0.44(0.07)	164.7(56.3)	123.6(84.4)	288.3(107.9)
High						
Untreated	0.06(0.06)	0.19(0.12)	0.25(0.12)	13.7(13.7)	432.4(385.1)	446.2(382.3)
Treated	0.28(0.10)	0.67(0.09)	0.78(0.07)	288.3(209.2)	1345.4(435.7)	1633.6(617.6)

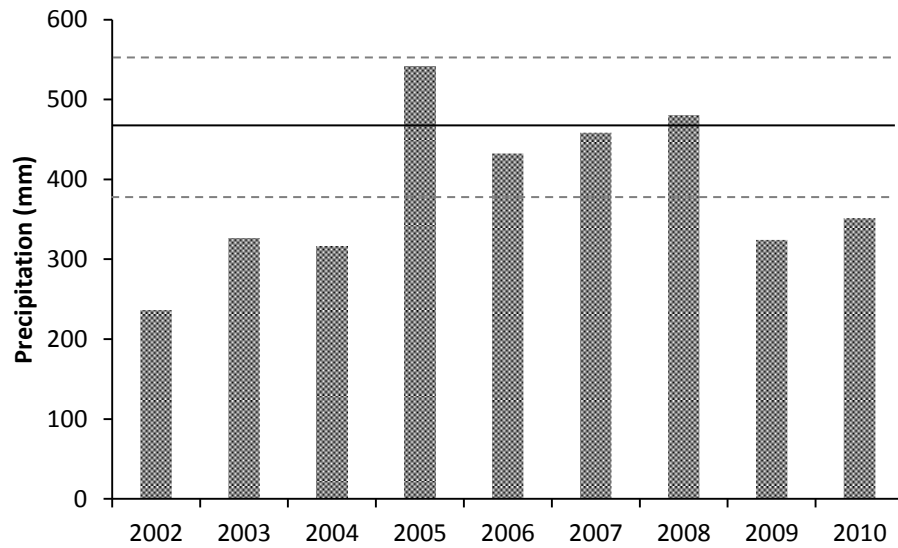


Figure 1. Precipitation data by water year from the period of post-fire recovery. Water year for a given year includes October through December of the previous year, and January through September of that year. Data are from the Heber Ranger Station in Heber, AZ, 12 km north of the study site. Solid line represents the 60-year average and dashed lines are one standard deviation.

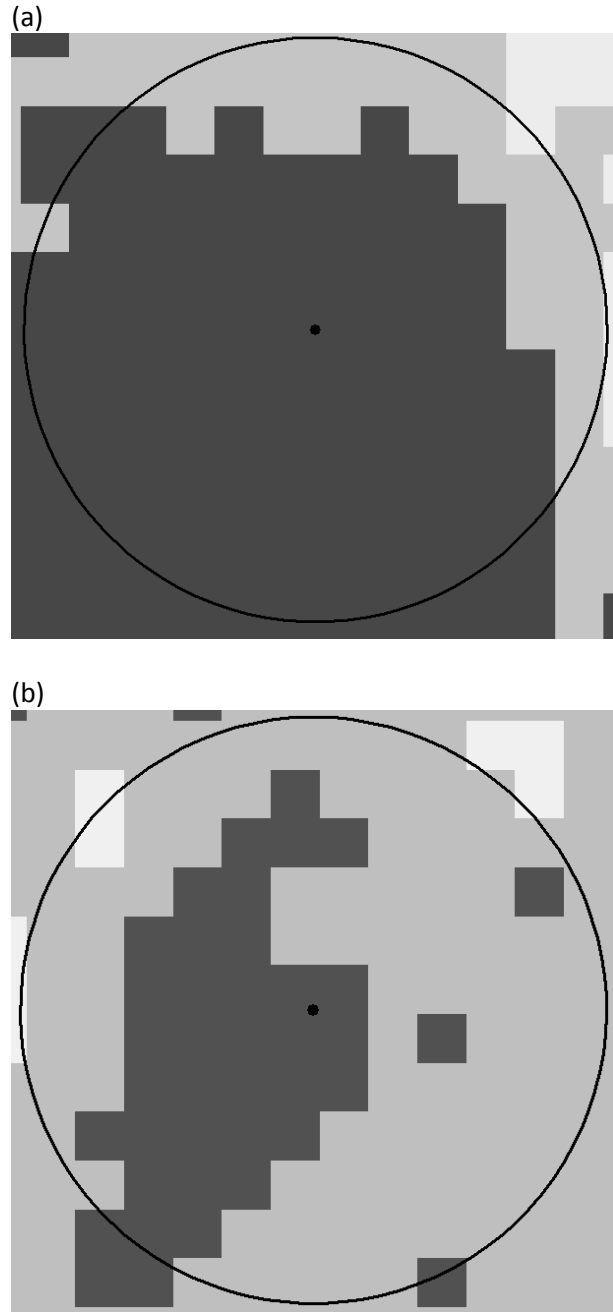


Figure 2. Example of how neighborhood severity analysis was conducted on pre-fire untreated (a) and treated (b) sites. Dots represent site centers and circles represent the area of potential seed contribution. The darkest shade of grey represents high severity, the lighter shade represents moderate severity and the lightest shade represents low severity.

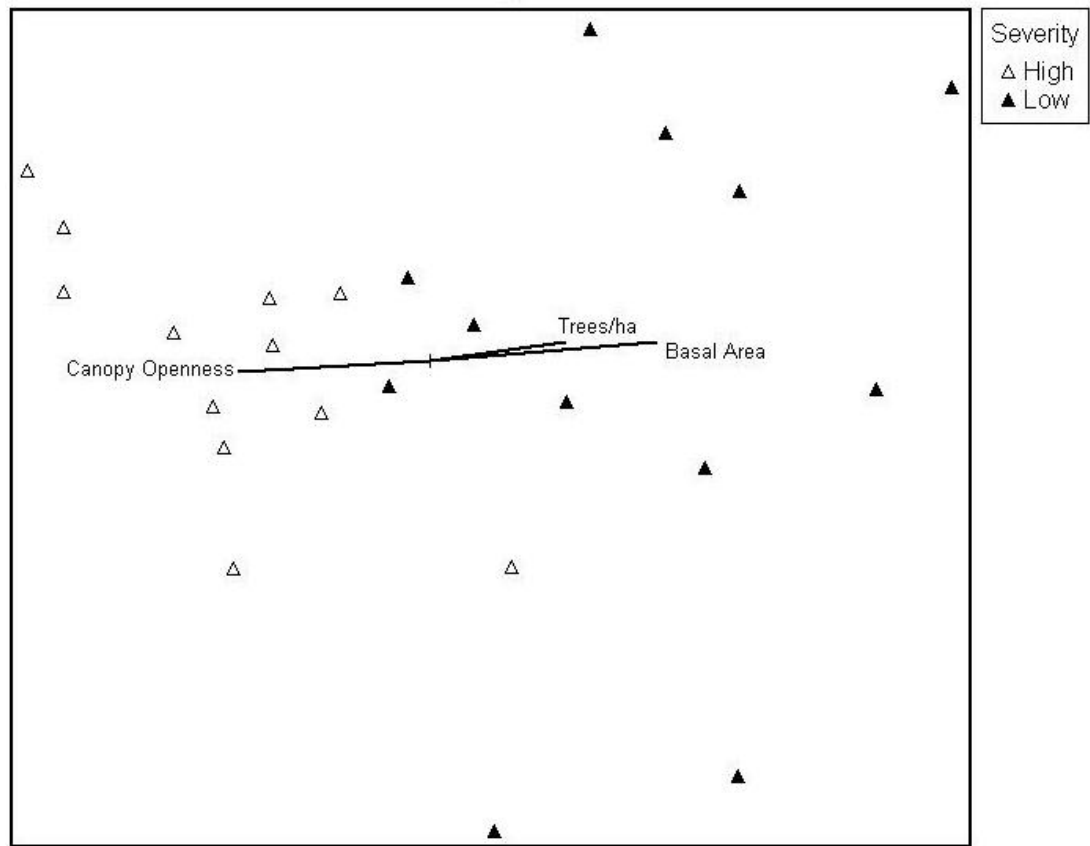


Figure 3. Ordination of 2010 plant communities by severity class with tree density, basal area and canopy openness overlaid as vectors. Stress: 8.435, p-value = 0.004, 3 dimensions.

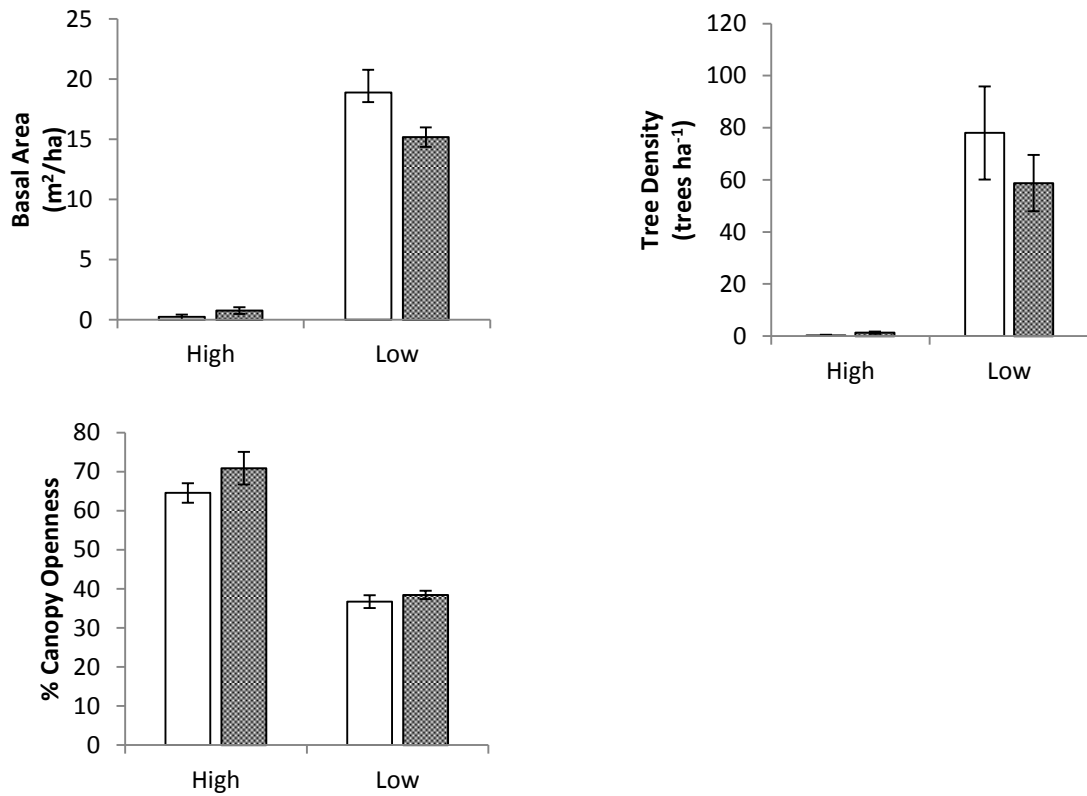


Figure 4. Overstory variables: basal area, tree density, canopy openness. Shaded bars represent pre-fire treated areas. All were significantly different by severity class, but none were significantly different by treatment within severity class.

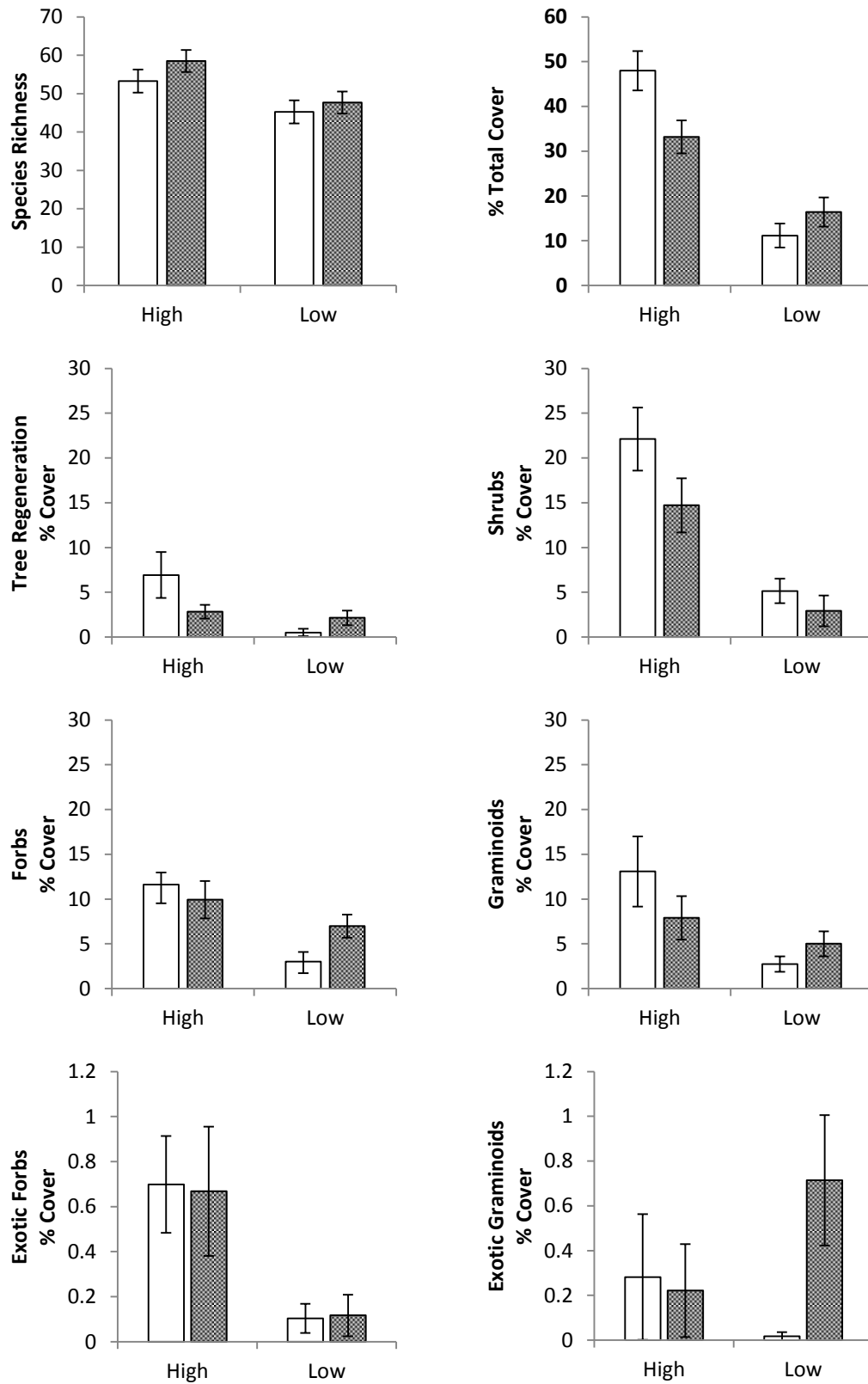


Figure 5. Species richness, total plant canopy cover, and cover by life form. Shaded bars represent pre-fire treated areas. Note differences in scale on the y-axis.

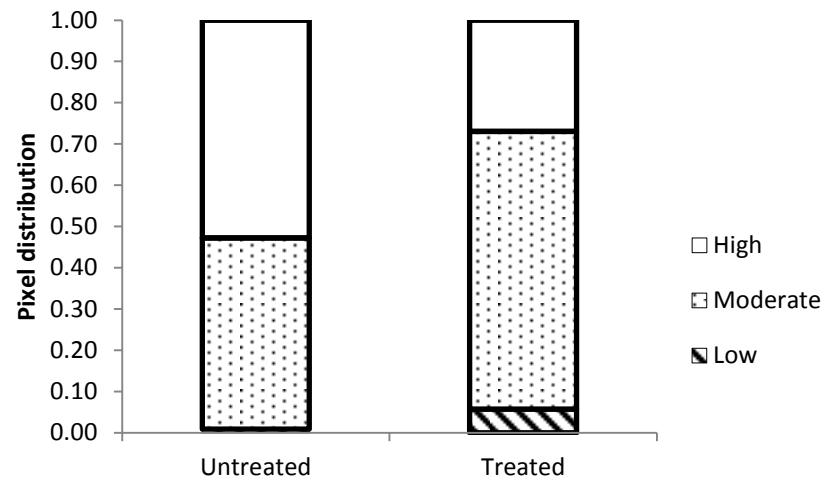


Figure 6. Neighborhood severity distribution for high severity treated and untreated areas.

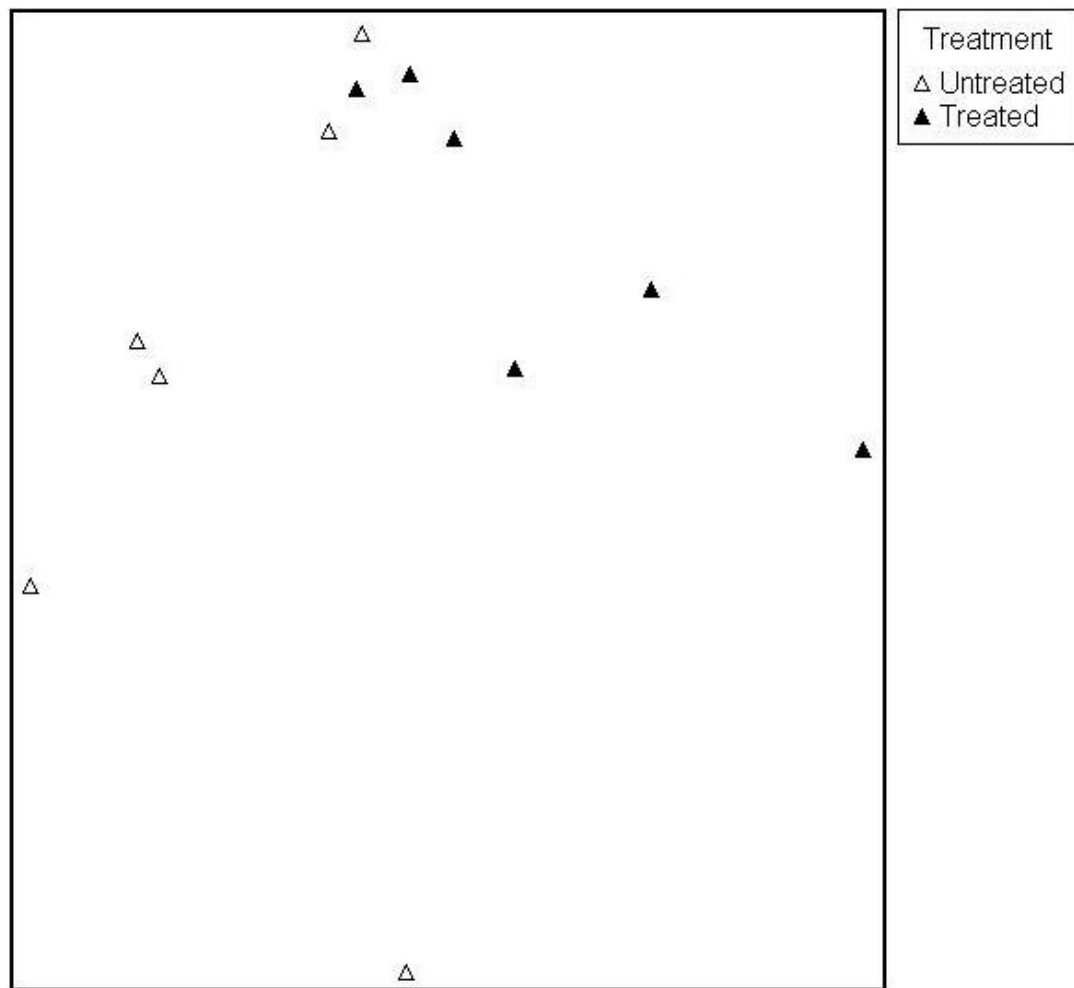


Figure 7. NMDS ordination of plant communities in high severity areas, by pre-fire treatment. Stress: 6.228, p-value = 0.028, 2 dimensions.

CHAPTER 4

Management Implications

Changes in vegetation structure and composition as a result of the 2002 Rodeo-Chediski Fire offer strong support for fuels reduction treatments in ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests of the Southwest. The post-fire effects of these treatments have important management implications at a number of scales. At the broadest scale, pre-fire treatments generally reduced fire severity, whereas untreated areas more often burned under high severity crown fire (Strom, 2005; Strom and Fulé, 2007). The preceding chapters documented how lower severity areas maintained overstory structure and mature ponderosa pine dominance. Severely burned areas generally lack overstory structure and many are shrub-dominated, some of which may remain persistent shrublands (Savage and Mast, 2005). This is significant because the loss of ponderosa pine as a foundation species in these areas may have significant cascading effects on other trophic levels (Ellison *et al.*, 2005). Furthermore, a few high severity areas have the potential to become doghair thickets of high density pine. These forests are at risk of another episode of high severity fire, thus perpetuating the cycle and potentially altering fire regimes.

High severity areas may also be an avenue for exotic species invasions, yet patterns of invasion in the Southwest have been highly variable. We observed significantly higher cover of exotic forbs in high severity areas compared to low severity burned areas on the White Mountain Apache Tribal (WMAT) land in 2010, whereas no difference was detected between high and low severity areas for 2004 or 2005. Although exotic cover was <3% for all years, this trend through time suggests that these species are maintaining a greater presence in the highly disturbed, high severity areas where there is generally more sunlight and potentially reduced competition from overstory trees for resources. On the Apache-Sitgreaves National Forest

(ASNF), mean exotic forb cover was also quite low for all years, at < 2.5%, but generally higher in untreated areas than in treated areas, and this difference approached significance. In addition, although overall exotic forb cover did not change dramatically in either study over time, there was an increase in the presence of several species across sampling plots. *Tragopogon dubius* Scop. (yellow salsify) increased in frequency by plot over the three measurement years in both study areas. *Verbascum thapsus* (common mullein) also increased in frequency on WMAT lands.

Overall exotic graminoid cover was highly variable in both study areas, and through time. Two species increased in either frequency or cover and may be cause for concern in the future. *Eragrostis curvula* (Shrad.) Nees (weeping lovegrass) increased in cover on WMAT lands in low severity areas. On ASNF lands, it first appeared on 18 of 80 measured plots in 2011. This grass is a robust perennial species that responds positively to fire (McFarland and Mitchell, 2000). In addition, the highly rhizomatous smooth brome (*Bromus inermis* Leyss.) increased in frequency on the ASNF in 2011. These two species are among the suite of cool-season graminoids that have been seeded in past decades in the Southwest (Wolfson and Sieg, In prep). Therefore, in areas where the goal is to maintain native species composition, we recommend using native seed only. However, any seeding has the potential to introduce exotic species as seed contaminants, and should be applied with caution (Keeley, 2006; Fowler *et al.*, 2008; Peppin *et al.*, 2010). In addition, these increases in exotic forb and graminoid frequency and cover over time suggest that long-term monitoring of high severity fire areas is important, particularly in order to track potentially problematic species.

Overall, the vegetative communities of more severely burned areas were relatively distinct from low severity areas. Yet, composition of understory herbaceous plant communities on the treated ASNF sites, which generally burned more severely than untreated sites, was converging with composition on untreated areas nine years post-fire. This convergence is likely

related to the proximity of the paired treated and untreated sites, such that the untreated, higher severity areas were never far from a lesser-burned edge. This suggests that treatments which minimize high severity patch size, and therefore distance to lesser-burned edge, may also minimize overall vegetation differences between severely burned and less severely burned areas. Therefore, conducting strategic treatments may be particularly important when treatment across an entire landscape is not feasible (Finney *et al.*, 2007).

These considerations relate to the broad scale effects of fire severity, which is generally mitigated by pre-fire treatment. The WMAT study design offers an exceptional opportunity to examine finer scale effects of treatment within severity class. Since weather conditions, topography and time of day also affect how severely areas burn, occasionally treated areas may burn severely. Ponderosa pine regeneration was less frequent in high severity areas that had not been treated before the wildfire than in the high severity pre-fire treated sites. In addition, pre-fire untreated sites had higher total plant cover and higher shrub cover. Lower frequency of pine regeneration in severely burned untreated areas was likely linked to the neighborhood severity surrounding the sampling sites, where untreated sites were surrounded by significantly greater area that burned severely than treated sites. Even within high severity fire areas, pre-fire treatments mitigated the effects of high severity fire by mitigating high severity patch size and increasing heterogeneity in the neighborhood of these sites. Ultimately, the untreated sites, which were generally in larger patches of high severity, are more likely to remain persistent shrublands. These areas, therefore, may be priorities for tree planting if the ultimate goal is to re-forest these areas.

Finally, post-fire seeding may have impacted native plant communities at both the broader scale of fire severity and the finer scale of treatment effects within severity class. Seed mixes were applied only in high severity fire areas on the WMAT lands, but throughout the ASNF

lands. Two exotic annual grass species, *Triticum aestivum* L. (common wheat) (seeded on the WMAT) and *Lolium perenne* L. (annual rye) (seeded on the A-S) were infrequent by 2005 and absent by 2010 and 2011. The exotic perennial grass *Festuca ovina* L. (sheep fescue) was also seeded on the ASNF, but was not detected until 2011, and then on only two plots. The remaining seeded species were native to the region, making it difficult to attribute their presence to either post-fire seeding or natural assembly. Further, we do not have any data from unseeded areas to assess how and if the early presence of these seeded species impacted the native plant communities in the long run. In light of this, the fact that the seeded annual cereal grains did exit the system as intended should not be simplistically interpreted as a success story; instead other studies that better evaluate the differences between seeded and non-seeded areas should be relied on for guidance (Stella *et al.* 2010; Peppin *et al.*, 2010).

Climate change has been linked with increases in high severity fire, and these fires are likely to continue to increase in the ponderosa pine type under the warmer and drier climate predicted for the Southwest (Westerling *et al.*, 2006; Seager *et al.*, 2007). In order to avoid the problematic outcomes examined in the last two chapters, such as exotic species proliferation or potential vegetation type conversions, management actions that reduce the incidence and extent of high severity crown fire and increase forest resilience will best protect native plant communities and vegetation types, on both broader and finer scales. Although restoring historical stand structures is one important way of creating more resilient ponderosa pine ecosystems, given the variability of the landscapes in the Southwest and the changing climate, a certain amount of flexibility may improve future successes. Adaptive management that incorporates a wide range of approaches to creating resilience can give managers a valuable toolbox for managing forests into the future (Millar *et al.*, 2007; Baron *et al.*, 2009).

REFERENCES

- Baron, J.S., Gunderson, L., Allen, C.D., Fleishman, E., McKenzie, D., Meyerson, L.A., Oropeza, J., Stephenson, N., 2009. Options for National Parks and Reserves for Adapting to Climate Change. *Environmental Management* 44, 1033-1042.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3, 479-486.
- Finney, M.A., Selia, R.C., McHugh, C.W., Ager, A.A., Bahro, B., Agee, J.K., 2007. Simulation of long-term landscape-level fuel treatment effects on large wildfires. *International Journal of Wildland Fire* 16, 712-727.
- Fowler, J.F., Sieg, C.H., Dickson, B.G., Saab, V., 2008. Exotic plant species diversity: Influence of roads and prescribed fire in Arizona ponderosa pine forests. *Rangeland Ecology & Management* 61, 284-293.
- Keeley, J.E., 2006. Fire management impacts on invasive plants in the western United States. *Conservation Biology* 20, 375-384.
- McFarland, J.B., Mitchell, R., 2000. Fire effects on weeping lovegrass tiller density and demographics. *Agronomy Journal* 92, 42-47.
- Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: Managing in the face of uncertainty. *Ecological Applications* 17, 2145-2151.
- Peppin, D., Fulé, P.Z., Sieg, C.H., Beyers, J.L., Hunter, M.E., 2010. Post-wildfire seeding in forests of the western United States: An evidence-based review. *Forest Ecology and Management* 260, 573-586.
- Savage, M., Mast, J.N., 2005. How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 35, 967-977.
- Seager, R., Ting, M.F., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.P., Harnik, N., Leetmaa, A., Lau, N.C., Li, C.H., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316, 1181-1184.
- Stella, K.A., Sieg, C.H., Fulé, P.Z., 2010. Minimal effectiveness of native and non-native seeding following three high-severity wildfires. *International Journal of Wildland Fire* 19, 746-758.
- Strom, B.A., 2005. Pre-fire treatment effects and post-fire forest dynamics on the Rodeo-Chediski burn area, Arizona. M.S. Thesis, School of Forestry, Flagstaff, AZ, Northern Arizona University.

Strom, B.A., Fulé, P.Z., 2007. Pre-wildfire fuel treatments affect long-term ponderosa pine forest dynamics. *International Journal of Wildland Fire* 16, 128-138.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940-943.

Wolfson, B.A.S., Sieg, C.H., In prep. 40-year post fire seeding trends in Arizona and New Mexico. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

APPENDICES

Appendix i. Species observed in 2004, 2005 and/or 2011 on the Apache-Sitgreaves National Forest study area. Life history strategies reported are from the USDA Plants database, abbreviated as A: annual or biennial, B: biennial, P: perennial. Exotic species have asterisks.

Species name	Authority	Life history	2004	2005	2011
Trees					
<i>Abies concolor</i>	(Gord. & Glend.) Lindl. ex Hildebr.	P		X	
<i>Juniperus deppeana</i>	Sted.	P	X	X	X
<i>Pinus ponderosa</i>	P. & C. Lawson	P	X	X	X
<i>Quercus gambelii</i>	Ntt.	P	X	X	X
<i>Rhus glabra</i>	L.	P	X		X
<i>Robinia neomexicana</i>	Gray	P	X	X	X
Shrubs					
<i>Agave parryi</i>	Engelm.	P	X	X	X
<i>Amelanchier alnifolia</i>	(Ntt.) Ntt. ex M. Roemer	P	X		
<i>Amelanchier utahensis</i>	Koehne	P		X	
<i>Amorpha fruticosa</i>	L.	P	X	X	X
<i>Arctostaphylos pringlei</i>	Parry	P	X	X	X
<i>Arctostaphylos pungens</i>	Knth	P	X	X	X
<i>Carphochaete bigelovii</i>	Gray	P		X	
<i>Ceanothus fendleri</i>	Gray	P	X	X	X
<i>Cercocarpus montanus</i>	Raf.	P	X	X	X
<i>Chrysothamnus depressus</i>	Ntt.	P	X	X	X
<i>Eriogonum wrightii</i>	Torr. ex Benth	P			X
<i>Fallugia paradoxa</i>	(D. Don) Endl. ex Torr.	P			X
<i>Gutierrezia sarothrae</i>	(Prsh) Britt. & Rsby	P	X	X	X
<i>Mahonia repens</i>	(Lindl.) G. Don	P	X	X	X
<i>Nolina microcarpa</i>	S. Wats.	P	X	X	X
<i>Purshia tridentata</i>	(Prsh) DC.	P	X		
<i>Quercus sp.</i>	L.	P	X	X	X
<i>Rhus trilobata</i>	Ntt.	P			X
<i>Rosa woodsii</i>	Lindl.	P	X	X	X
<i>Yucca angustissima</i>	Engelm. ex Trel.	P	X	X	X
<i>Yucca elata</i>	(Engelm.) Engelm.	P	X		
Forbs					
<i>Achillea millefolium</i>	L.	P	X	X	X
<i>Ageratina herbacea</i>	(Gray) King & H.E. Robins.	P	X	X	X
<i>Allium cernuum</i>	Roth	P			X
<i>Allium sp.</i>	L.	P		X	
<i>Amaranthus blitoides*</i>	S. Wats.	A	X		
<i>Amaranthus sp.</i>	L.	A	X	X	X

Species name	Authority	Life history	2004	2005	2011
<i>Ambrosia acanthicarpa</i>	Hook.	A	X	X	
<i>Ambrosia psilostachya</i>	DC.	P	X	X	X
<i>Antennaria marginata</i>	Greene	P	X	X	
<i>Antennaria parviflora</i>	Ntt.	P	X	X	X
<i>Antennaria rosulata</i>	Rydb.	P	X		
<i>Arabis sp.</i>	L.	U	X		
<i>Arenaria lanuginosa</i>	(Michx.) Rohrb.	P	X	X	X
<i>Argemone minuta ssp. rotundata</i>	Dr. & Hilg.	P	X	X	
<i>Artemisia campestris</i>	L.	P	X	X	X
<i>Artemisia carruthii</i>	Wood ex Carrth.	P	X	X	X
<i>Artemisia dracunculus</i>	L.	P	X	X	
<i>Artemisia ludoviciana</i>	(Ntt.) Keck	P	X	X	X
<i>Asclepias asperula ssp. asperula</i>	(Dcne.) Woods.	P	X	X	X
<i>Asclepias subverticillata</i>	(Gray) Vail	P			X
<i>Asclepias tuberosa</i>	L.	P	X		
<i>Astragalus gilensis</i>	Greene	P		X	X
<i>Astragalus hallii</i>	Gray	P	X	X	X
<i>Astragalus humistratus</i>	Gray	P	X	X	X
<i>Astragalus mollissimus</i>	Torr.	P	X	X	X
<i>Astragalus sp.</i>	L.	P	X	X	X
<i>Astragalus tephrodes</i>	Gray	P	X	X	X
<i>Bahia dissecta</i>	(Gray) Britt.	B	X	X	X
<i>Bassia hyssopifolia*</i>	(Pallas) Kntz	A		X	
<i>Bassia scoparia*</i>	(L.) A.J. Scott	A	X		
<i>Brickellia betonicifolia</i>	Gray	P	X		X
<i>Brickellia californica</i>	(Torr. & Gray) Gray	P	X		
<i>Brickellia eptarioides var. chlorolepis</i>	(L.) Shinnars	P	X	X	X
<i>Brickellia grandiflora</i>	(Hook.) Ntt.	P	X	X	X
<i>Calliandra humilis</i>	Benth.	P	X	X	X
<i>Calochortus nuttallii</i>	Torr. & Gray	P		X	
<i>Castilleja sulphurea</i>	Rydb.	P			X
<i>Castilleja sp.</i>	Mtis ex L. f.	P	X	X	X
<i>Chaetopappa ericoides</i>	(Torr.) Nesom	P	X	X	X
<i>Chamaesyce glyptosperma</i>	(Engelm.) Small	A			X
<i>Chamaesyce serpyllifolia</i>	(Pers.) Small	A	X	X	X
<i>Chenopodium album*</i>	L.	A	X	X	
<i>Chenopodium botrys*</i>	L.	A	X		
<i>Chenopodium desiccatum</i>	A. Nels.	A	X		
<i>Chenopodium graveolens</i>	Willd.	A	X	X	X
<i>Chenopodium leptophyllum</i>	(Moq.) Ntt. ex S. Wats.	A	X	X	

Species name	Authority	Life history	2004	2005	2011
<i>Chenopodium sp.</i>	L.	A		X	X
<i>Cirsium arizonicum</i>	(Gray) Petrak	P	X		
<i>Cirsium rothrockii</i>	(Gray) Petrak	B	X	X	
<i>Cirsium sp.</i>	P. Mill.			X	X
<i>Cirsium vulgare*</i>	(Savi) Ten	B	X	X	X
<i>Cirsium wheeleri</i>	(Gray) Petrak	P	X	X	X
<i>Cologania angustifolia</i>	Knth	P	X	X	X
<i>Comandra umbellata</i>	(L.) Ntt.	P	X	X	X
<i>Commelina dianthifolia</i>	Delile	P	X	X	X
<i>Conyza canadensis</i>	(L.) Cronq.	A	X	X	X
<i>Cordylanthus wrightii</i>	Gray	A	X	X	X
<i>Coreopsis tinctoria</i>	Ntt.	ABP	X	X	
<i>Cryptantha cinerea</i>	(Greene) Cronq.	P	X	X	X
<i>Cryptantha fendleri</i>	(Gray) Greene	A	X	X	X
<i>Dalea albiflora</i>	Gray	P	X	X	X
<i>Dalea candida</i>	Michx. ex Willd.	P	X	X	X
<i>Dalea sp.</i>	L.	U			X
<i>Dalea filiformis</i>	Gray	A	X		
<i>Dalea polygonoides</i>	Gray	A	X		
<i>Descurainia sp.</i>	Webb & Berth. (Bernh. ex Fisch. & C.A. Mey.)	U		X	
<i>Descurainia incana</i>	Dorn	AB	X	X	X
<i>Desmanthus cooleyi</i>	(Eat.) Trel.	P	X	X	X
<i>Desmodium grahamii</i>	Gray	P		X	
<i>Dracocephalum parviflorum</i>	Ntt. (Cham. & Schlecht.) Fenzl ex	AB		X	X
<i>Drymaria leptophylla</i>	Rohrb.	A	X	X	
<i>Dyssodia papposa</i>	(Vent.) A.S. Hitchc.	A	X	X	X
<i>Echeandia flavescens</i>	(J.A. & J.H. Schltes) Crden	P	X	X	X
<i>Epilobium brachycarpum</i>	K. Presl.	A	X	X	X
<i>Erigeron canus</i>	Gray	P	X	X	
<i>Erigeron colomexicanus</i>	A. Nels.	B	X	X	X
<i>Erigeron divergens</i>	Torr. & Gray	B	X	X	X
<i>Erigeron flagellaris</i>	Gray	B	X	X	X
<i>Erigeron formosissimus</i>	Greene	P		X	X
<i>Erigeron sp.</i>	L.	P			X
<i>Erigeron neomexicanus</i>	Gray	P	X	X	X
<i>Erigeron speciosus</i>	(Lindl.) DC.	P	X	X	X
<i>Eriogonum alatum</i>	Torr.	P	X	X	X
<i>Eriogonum corymbosum</i>	Benth	P	X		
<i>Eriogonum polycladon</i>	Benth.	A	X	X	X
<i>Eriogonum racemosum</i>	Ntt.	P	X	X	X
<i>Erodium cicutarium*</i>	(L.) L'Hér. ex Ait.	A	X	X	X

Species name	Authority	Life history	2004	2005	2011
<i>Escobaria vivipara</i>	(Ntt.) Bxbam	P	X	X	X
<i>Euphorbia brachycera</i>	Engelm.	P			X
<i>Euphorbia dentata</i>	Michx.	A	X	X	
<i>Evolvulus sericeus</i>	Sw.	P	X	X	X
<i>Frasera speciosa</i>	Dogl. ex Griseb.	P		X	
<i>Froelichia gracilis</i>	(Ntt.) Moq.	A	X	X	
<i>Gaura hexandra</i>	Ortega	A	X	X	X
<i>Gayophytum diffusum</i>	Torr. & Gray	A	X	X	X
<i>Geranium caespitosum</i>	James	P	X	X	X
<i>Hedeoma drummondii</i>	Benth.	P	X	X	X
<i>Hedeoma hyssopifolia</i>	Gray	P	X	X	X
<i>Helianthus annuus</i>	L.	A	X	X	X
<i>Heliomeris multiflora</i>	Ntt.	P	X	X	X
<i>Heterosperma pinnatum</i>	Cav.	A	X		
<i>Heterotheca subaxillaris</i>	(Lam.) Britt. & Rsby	A	X	X	X
<i>Heterotheca villosa</i>	(Prsh) Shinnars	P	X	X	X
<i>Hieracium fendleri</i>	Schltz-Bip.	P	X	X	X
<i>Houstonia wrightii</i>	Gray	P	X	X	X
<i>Hymenopappus filifolius</i>	Hook.	P	X	X	X
<i>Hymenopappus mexicanus</i>	Gray	P	X	X	X
<i>Hymenothrix wrightii</i>	Gray	PB	X	X	X
<i>Hymenoxys bigelovii</i>	(Gray) Parker	P	X	X	X
<i>Hymenoxys cooperi</i>	(Gray) Cockerell	P		X	
<i>Hymenoxys hoopesii</i>	(Gray) Bierner	P	X		
<i>Ipomoea costellata</i>	Torr.	A	X	X	X
<i>Ipomoea cristulata</i>	Hallier f.	A	X	X	X
<i>Ipomoea sp.</i>	L.		X	X	X
<i>Ipomoea plummerae</i>	Gray	P	X	X	X
<i>Ipomopsis aggregata</i>	(Prsh) V. Grant	B	X	X	X
<i>Ipomopsis multiflora</i>	(Ntt.) V. Grant	P	X	X	X
<i>Iris missouriensis</i>	Ntt.	P	X		
<i>Lactuca serriola*</i>	L.	P	X	X	X
<i>Lactuca tatarica</i>	(L.) C.A. Mey.	PB		X	X
<i>Laennecia scheideana</i>	(Less.) Nesom	A	X	X	X
<i>Lappula occidentalis</i>	(S. Wats.) Greene	AB		X	X
<i>Lathyrus eucosmus</i>	Btters & St. John	P	X	X	X
<i>Lathyrus gaminifolius</i>	(S. Wats.) White	P			X
<i>Lathyrus sp.</i>	L.	P		X	
<i>Lathyrus laetivirens</i>	Greene ex Rydb.	P		X	X
<i>Lathyrus lanszwertii var. leucanthus</i>	Kellogg	P		X	X
<i>Lepidium densiflorum</i>	Schrad.	A	X	X	X
<i>Linum aristatum</i>	Engelm.	A		X	

Species name	Authority	Life history	2004	2005	2011
<i>Linum australe</i>	Heller	A			X
<i>Linum lewisii</i> var. <i>lewisii</i>	Prsh	P	X		
<i>Linum neomexicanum</i>	Greene	ABP	X	X	X
<i>Lithospermum cobrense</i>	Greene	P	X	X	
<i>Lithospermum</i> sp.	L.	P	X	X	
<i>Lithospermum incisum</i>	Lehm.	P	X		
<i>Lithospermum multiflorum</i>	Torr. ex Gray	P	X	X	X
<i>Lotus plebeius</i>	(Brandeg.) Barneby	P	X		
<i>Lotus</i> sp.	L.	P	X		
<i>Lotus wrightii</i>	(Gray) Greene	P	X	X	X
<i>Lupinus hillii</i>	Greene	P	X	X	X
<i>Lupinus kingii</i>	S. Wats.	A	X		X
<i>Machaeranthera canescens</i>	(Prsh) Gray	P	X	X	
<i>Machaeranthera gracilis</i>	(Ntt.) Shinners	A	X	X	X
<i>Malva neglecta</i> *	Wallr.	ABP	X	X	X
<i>Medicago lupulina</i> *	L.	P	X	X	X
<i>Medicago sativa</i> *	L.	P	X	X	
<i>Melilotus officinalis</i> *	(L.) Lam.	ABP	X	X	X
<i>Microsteris gracilis</i>	(Hook.) Green	A	X	X	
<i>Mimulus rubellus</i>	Gray	A		X	
<i>Mirabilis decipiens</i>	(Standl.) Standl.	P	X	X	X
<i>Mirabilis linearis</i>	(Prsh) Heimerl.	P	X	X	X
<i>Monarda pectinata</i>	Ntt.	P	X	X	X
<i>Monardella glauca</i>	Greene	P		X	
<i>Nicotiana attenuata</i>	Torr. ex S. Wats.	A	X	X	
<i>Noccaea montana</i>	(L.) F.K. Mey.	P	X	X	X
<i>Oenothera coronopifolia</i>	Torr. & Gray	P		X	
<i>Oenothera elata</i>	Knth	PB	X	X	
<i>Oenothera laciniata</i>	Hill	AP			X
<i>Oenothera</i> sp.	L.	P			X
<i>Oenothera pubescens</i>	Willd. ex Spreng.	AP	X	X	
<i>Opuntia</i> sp.	P. Mill.	P	X	X	X
<i>Oreochrysum parryi</i>	(Gray) Rydb.	P		X	
<i>Orobanche ludoviciana</i>	Ntt.	A		X	
<i>Oxalis decaphylla</i>	Knth	P	X	X	X
<i>Oxalis</i> sp.	L.	U	X	X	
	(Torr. & Gray ex Gray) W.A.				
<i>Packera multilobata</i>	Weber & A. Löve	P			X
<i>Packera neomexicana</i>	(Gray) W.A. Weber & A. Löve	P	X	X	X
<i>Pedicularis centranthera</i>	Gray	P	X	X	X
<i>Pennellia longifolia</i>	(Benth.) Rollins	B	X	X	X
<i>Penstemon barbatus</i>	(Cav.) Roth	P	X	X	X
<i>Penstemon linarioides</i>	Gray	P	X	X	X

Species name	Authority	Life history	2004	2005	2011
<i>Penstemon pachyphyllus</i>	Gray ex Rydb.	P		X	
<i>Penstemon palmeri</i>	Gray	P		X	X
<i>Penstemon sp.</i>	Schmidel	P			X
<i>Penstemon virgatus</i>	Gray	P	X	X	X
<i>Pericome caudata</i>	Gray	P		X	
	(Greene ex Brand) Greene ex J.T.				
<i>Phacelia egena</i>	Howell	P	X		
<i>Phacelia heterophylla</i>	Prsh	PB		X	X
<i>Phaseolus angustissimus</i>	Gray	P	X	X	X
<i>Phaseolus grayanus</i>	Woot. & Stadl.	P		X	X
<i>Phemeranthus parviflorus</i>	(Ntt.) Kiger	P			X
<i>Phemeranthus confertiflorus</i>	(Greene) Hershkovitz	P	X	X	
<i>Phlox longifolia</i>	Ntt.	P	X	X	X
<i>Phlox speciosa</i>	Prsh	P	X	X	
<i>Physalis hederifolia</i>	Gray	P	X	X	X
<i>Plantago argyraea</i>	Morris	A	X	X	X
<i>Plantago patagonica</i>	Jacq.	A		X	X
<i>Polygala obscura</i>	Benth.	P			X
<i>Polygonum aviculare*</i>	L.	AP	X	X	X
<i>Polygonum convolvulus*</i>	L.	A		X	
<i>Polygonum douglasii</i>	Greene	A	X	X	X
<i>Polygonum lapathifolium</i>	L.	A	X		
<i>Portulaca halimoides</i>	L.	A			X
<i>Portulaca oleracea</i>	L.	A	X	X	X
<i>Potentilla crinite</i>	Gray	P	X	X	X
<i>Potentilla sp.</i>	L.	P			X
<i>Potentilla subviscosa</i>	Greene	P		X	
<i>Potentilla thurberi</i>	Gray	P	X		
<i>Pseudocymopterus montanus</i>	(Gray) Colt. & Rose	P	X	X	X
<i>Pseudognaphalium macounii</i>	(Greene) Kartesz	AB	X	X	X
<i>Psoralidium lanceolatum</i>	(Prsh) Rydb.	P	X	X	X
<i>Psoralidium tenuiflorum</i>	(Prsh) Rydb.	P	X	X	X
<i>Pyrrocoma crocea</i>	(Gray) Greene	P		X	X
<i>Rorippa sylvestris*</i>	(L.) Bess.	P		X	X
<i>Rudbeckia hirta</i>	L.	ABP	X		
<i>Rumex acetosella*</i>	L.	P	X	X	X
<i>Rumex crispus*</i>	L.	P	X	X	X
<i>Salsola tragus*</i>	L.	A	X	X	
<i>Sanguisorba minor*</i>	Scop.	P	X	X	
<i>Saxifraga rhomboidea</i>	Greene	P		X	X
<i>Schkuhria multiflora</i>	Hook. & Arn.	A	X		
<i>Schoenocrambe linearifolia</i>	(Gray) Rollins	P	X	X	X

Species name	Authority	Life history	2004	2005	2011
<i>Senecio eremophilus</i>	Richards	P		X	
<i>Senecio flaccidus</i>	Less.	P	X	X	X
<i>Senecio spartioides</i>	Torr. & Gray	P	X		
<i>Senecio wootonii</i>	Greene	P	X		
<i>Silene antirrhina</i>	L.	A	X	X	X
<i>Silene lacinata</i>	Cav.	P	X	X	X
<i>Sisymbrium altissimum</i> *	L.	AB		X	X
<i>Solanum americanum</i>	P. Mill.	P	X	X	
<i>Solidago sp.</i>	L.	P	X	X	X
<i>Sonchus sp.</i> *	L.	P		X	
<i>Sphaeralcea sp.</i>	St.-Hil.	P	X	X	
<i>Sphaeralcea coccinea</i>	(Ntt.) Rydb.	P			X
<i>Sphaeralcea fendleri</i>	Gray	P	X	X	X
<i>Sphaeralcea parviflora</i>	A. Nels.	P	X	X	
<i>Symphyotrichum falcatum</i>	(Lindl.) Nesom.	P	X	X	X
<i>Tagetes micrantha</i>	Cav.	A	X		X
<i>Taraxacum officinale</i> *	G.H.Weber ex Wiggers	P	X	X	X
<i>Tetrandeum acaulis</i>	(Prsh) Greene	P	X		
<i>Tetrandeum ivesiana</i>	Greene	P	X	X	X
<i>Thalictrum fendleri</i>	Engelm. ex Gray	P	X	X	
<i>Thelesperma megapotamicum</i>	(Spreng.) Kntze	P	X	X	X
<i>Thermopsis montana</i> var. <i>montana</i>	Ntt.	P	X	X	X
<i>Townsendia exscapa</i>	(Richards.) Porter	P	X	X	X
<i>Tradescantia pinetorum</i>	Greene	P	X	X	X
<i>Tragia ramosa</i>	Torr.	P	X	X	X
<i>Tragopogon dubius</i> *	Scop.	AB	X	X	X
<i>Trifolium sp.</i>	L.	P	X		
<i>Verbascum thapsus</i> *	L.	B	X	X	X
<i>Verbena bracteata</i>	Cav. ex Lag. & Rodr.	P	X	X	X
<i>Vicia Americana</i>	Mhl. ex Willd.	P	X	X	X
<i>Vicia pulchella</i>	Knth	P	X	X	X
<i>Wyethia arizonica</i>	Gray	P	X	X	X
Graminoids					
<i>Achnatherum hymenoides</i>	(Roemer & J.A. Schltes) Barkworth	P		X	
<i>Achnatherum nelsonii</i>	(Scribn.) Barkworth	P	X		
<i>Agropyron desertorum</i> *	(Fisch. ex Link) J.A. Schltes	P		X	
<i>Agrostis sp.</i>	L.	U			X
<i>Agrostis scabra</i>	Willd.	P	X	X	X
<i>Andropogon gerardii</i>	Vitman	P		X	

Species name	Authority	Life history	2004	2005	2011
<i>Aristida arizonica</i>	Vasey	P	X	X	X
<i>Aristida purpurea</i>	Ntt.	P	X		X
<i>Aristida schiedeana</i> var. <i>orcuttiana</i>	Trin. & Rpr.	P	X	X	X
<i>Avena fatua</i> *	L.	A		X	
<i>Blepharoneuron tricholepis</i>	(Torr.) Nash	P	X	X	X
<i>Bouteloua curtipendula</i>	(Michx.) Torr.	P	X	X	X
<i>Bouteloua eriopoda</i>	(Torr.) Torr.	P	X		
<i>Bouteloua gracilis</i>	(Willd. ex Knth) Lag. ex Griffiths	P	X	X	X
<i>Bouteloua hirsuta</i>	Lag.	P	X		X
<i>Bromus carinatus</i>	Hook. & Arn.	P	X	X	X
<i>Bromus ciliates</i>	L.	P		X	X
<i>Bromus inermis</i> *	Leyss.	P	X	X	X
<i>Bromus japonicus</i> *	Thnb.	A	X	X	X
<i>Bromus racemosus</i> *	L.	A		X	
<i>Bromus tectorum</i> *	L.	A	X	X	X
<i>Bulbostylis funckii</i>	(Sted.) C.B. Clarke	A		X	
<i>Carex</i> sp.	L.	P	X	X	X
<i>Carex geophila</i>	Mackenzie	P		X	
<i>Cyperus</i> sp.	L.	P	X		X
<i>Cyperus fendlerianus</i>	Boeckl.	P	X	X	X
<i>Dactylis glomerata</i> *	L.	P	X	X	X
<i>Dichanthelium linearifolium</i>	(Scribn. ex Nash) Gold	P	X		
<i>Dichanthelium oligosanthes</i>	(J. A. Schltes) Gold	P		X	X
<i>Echinochloa crus-galli</i> *	(L.) Beav.	A		X	
<i>Elymus elymoides</i>	(Raf.) Swezey	P	X	X	X
<i>Elymus glaucus</i>	Bckl.	P	X		
<i>Elymus trachycaulus</i>	(Link) Gold ex Shinnars	P	X	X	X
<i>Eragrostis curvula</i> *	(Schrud.) Nees	P			X
<i>Eragrostis mexicana</i>	(Hornem.) Link	A	X	X	
<i>Eragrostis pectinacea</i> var. <i>pectinacea</i>	(Michx.) Nees ex Sted	A	X	X	X
<i>Festuca arizonica</i>	Vasey	P	X		
<i>Festuca ovina</i>	L.	P			X
<i>Festuca sororia</i>	Piper	P			X
<i>Festuca</i> sp.	L.	P		X	
<i>Hesperostipa comata</i>	(Trin. & Rpr.) Barkworth	P	X	X	X
<i>Hordeum jubatum</i>	L.	P	X	X	X
<i>Juncus bufonius</i>	L.	A		X	
<i>Juncus confuses</i>	Coville	P	X	X	
<i>Juncus mexicanus</i>	Willd. ex J.A. & J.H. Schltes	P		X	
<i>Juncus tenuis</i>	Willd.	P			X
<i>Koeleria macrantha</i>	(Ledeb.) J.A. Schltes	P	X	X	X

Species name	Authority	Life history	2004	2005	2011
<i>Lolium perenne</i> *	L.	AP	X	X	
<i>Lycurus phleoides</i>	Knth	P			X
<i>Lycurus setosus</i>	(Ntt.) C.G. Reeder	P	X		
<i>Monroa squarrosa</i>	(Ntt.) Torr.	A	X		
<i>Muhlenbergia longiligula</i>	A.S. Hitchc.	P	X	X	X
<i>Muhlenbergia minutissima</i>	(Sted.) Swallen	A	X	X	X
<i>Muhlenbergia montana</i>	(Ntt.) A.S. Hitchc.	P	X	X	X
<i>Muhlenbergia rigens</i>	(Benth.) A.S. Hitchc.	P	X	X	X
<i>Muhlenbergia virescens</i>	(Knth) Knth	P	X	X	X
<i>Muhlenbergia wrightii</i>	Vasey ex Colt.	P	X	X	X
<i>Nassella viridula</i>	(Trin.) Barkworth	P	X		
<i>Panicum bulbosum</i>	Knth	P	X	X	X
<i>Panicum virgatum</i>	L.	P		X	
<i>Pascopyrum smithii</i>	(Rydb.) A. Löve	P	X	X	X
<i>Piptochaetium pringlei</i>	(Beal) Parodi	P	X	X	X
<i>Pleuraphis jamesii</i>	Torr.	P			X
<i>Poa compressa</i> *	L.	P		X	X
<i>Poa fendleriana</i>	(Sted.) Vasey	P	X	X	X
<i>Poa pratensis</i> *	L.	P	X	X	X
<i>Schedonorus pratensis</i> *	(Hds.) Beav.	P		X	
<i>Schizachyrium scoparium</i>	(Michx.) Nash	P	X	X	X
<i>Sorghastrum nutans</i>	(L.) Nash	P		X	X
<i>Sporobolus cryptandrus</i>	(Torr.) Gray	P	X	X	X
<i>Sporobolus interruptus</i>	Vasey	P	X	X	X
<i>Triticum aestivum</i> *	L.	A	X	X	
<i>Vulpia octoflora</i>	(Walt.) Rydb.	A	X	X	X

Appendix ii. Species list for 2010 measurements on White Mountain Apache Tribal lands.
Exotic species are asterisked.

Species name	Authority
Trees	
<i>Abies concolor</i>	(Gord. & Glend.) Lindl. ex Hildebr.
<i>Frangula californica</i>	(Eschsch) A. Gray
<i>Juglans major</i>	(Torr.) Heller
<i>Juniperus deppeana</i>	Steud.
<i>Pinus leiophylla</i> var. <i>chihuahuana</i>	Schiede & Deppe
<i>Pinus ponderosa</i>	P. & C. Lawson
<i>Pseudotsuga menziesii</i>	(Mirbel) Franco
<i>Quercus gambelii</i>	Nutt.
<i>Quercus</i> sp.	L.
<i>Rhus glabra</i>	L.
<i>Robinia neomexicana</i>	Gray
Shrubs	
<i>Amelanchier utahensis</i>	Koehne
<i>Arctostaphylos pringlei</i>	Parry
<i>Arctostaphylos pungens</i>	Kunth
<i>Baccharis pteronioides</i>	DC.
<i>Carphochaete bigelovii</i>	Gray
<i>Ceanothus fendleri</i>	Gray
<i>Cercocarpus montanus</i>	Raf.
<i>Garrya flavescens</i>	S. Wats.
<i>Lonicera arizonica</i>	Rehd.
<i>Mahonia repens</i>	(Lindl.) G. Don
<i>Nolina microcarpa</i>	S. Wats.
<i>Paxistima myrsinites</i>	(Pursh) Raf.
<i>Purshia tridentata</i>	(Pursh) DC.
<i>Quercus grisea</i>	Liebm.
<i>Rhus trilobata</i>	Nutt.
<i>Rosa woodsii</i>	Lindl.
<i>Rubus idaeus</i>	L.
<i>Rubus parviflorus</i>	Nutt.
<i>Symphoricarpos oreophilus</i>	Gray
<i>Tetradymia</i> sp.	DC.
<i>Yucca angustissima</i>	Engelm. ex Trel.
<i>Yucca baccata</i>	Torr.
Forbs	
<i>Acalypha neomexicanum</i>	Mull. Arg.
<i>Achillea millefolium</i>	L.
<i>Ageratina herbacea</i>	(Gray) King & H.E. Robins.

Species name	Authority
<i>Ageratina</i> sp.	
<i>Amaranthus powellii</i>	S. Wats.
<i>Amaranthus</i> sp.	L.
<i>Ambrosia acanthicarpa</i>	Hook.
<i>Ambrosia psilostachya</i>	DC.
<i>Anaphalis margaritacea</i>	(L.) Benth.
<i>Antennaria marginata</i>	Greene
<i>Antennaria parviflora</i>	Nutt.
<i>Apocynum androsaemifolium</i>	L.
<i>Arabis</i> sp.	L.
<i>Arenaria lanuginosa</i>	(Michx.) Rohrb.
<i>Arenaria lanuginosa</i> ssp. <i>saxosa</i>	(Michx.) Rohrb.
<i>Argemone munita</i>	Dur. & Hilg.
<i>Artemisia capestris</i>	L.
<i>Artemisia carruthii</i>	Wood ex Carruth.
<i>Artemisia ludoviciana</i>	(Nutt.) Keck
<i>Asclepias asperula</i>	(Dcne.) Woods.
<i>Asclepias</i> sp.	L.
<i>Asclepias tuberosa</i>	L.
<i>Astragalus fucatus</i>	Barneby
<i>Astragalus hallii</i>	Gray
<i>Astragalus</i> sp.	L.
<i>Astragalus tephrodes</i>	Gray
<i>Bahia dissecta</i>	(Gray) Britt.
<i>Brickellia betonicifolia</i>	Gray
<i>Brickellia eupatorioides</i> var. <i>chlorolepis</i>	(L.) Shinnars
<i>Brickellia grandiflora</i>	(Hook.) Nutt.
<i>Calliandra humilis</i>	Benth.
<i>Calliandra humilis</i> var. <i>humilis</i>	Benth.
<i>Calliandra humilis</i> var. <i>recitulata</i>	Benth.
<i>Castilleja miniata</i>	Dougl. ex Hook.
<i>Castilleja</i> sp.	Mutis ex L. f.
<i>Chaetopappa ericoides</i>	(Torr.) Nesom
<i>Chamaesyce revoluta</i>	(Engelm.) Small
<i>Chamaesyce serpyllifloia</i>	(Pers.) Small
<i>Chenopodium graveolens</i>	Willd.
<i>Chenopodium</i> sp.	L.
<i>Cirsium arizonicum</i>	(Gray) Petrak
<i>Cirsium vulgare</i> *	(Savi) Ten
<i>Cirsium wheeleri</i>	(Gray) Petrak
<i>Collinsia parviflora</i>	Lindl.

Species name	Authority
<i>Cologania angustifolia</i>	Kunth
<i>Comandra umbellata</i>	(L.) Nutt.
<i>Commelina dianthifolia</i>	Delile
<i>Conyza canadensis</i>	(L.) Cronq.
<i>Cordylanthus wrightii</i>	Gray
<i>Cylindropuntia</i> sp.	
<i>Dalea albiflora</i>	Gray
<i>Dalea candida</i>	Michx. ex Willd.
<i>Dalea</i> sp.	L.
<i>Desmanthus cooleyi</i>	(Eat.) Trel.
<i>Desmodium arizonicum</i>	S. Watson
<i>Desmodium grahamii</i>	Gray
<i>Drymaria leptophylla</i>	(Cham. & Schlecht.) Fenzl ex Rohrb.
<i>Dyssodia papposa</i>	(Vent.) A.S. Hitchc.
<i>Echeandia flavescens</i>	(J.A. & J.H. Schultes) Cruden
<i>Epilobium brachycarpum</i>	K. Presl.
<i>Epilobium ciliatum</i> ssp. <i>ciliatum</i>	Raf.
<i>Epilobium</i> sp.	
<i>Equisetum laevigatum</i>	A. Braun
<i>Erigeron colomexicanus</i>	A. Nels.
<i>Erigeron divergens</i>	Torr. & Gray
<i>Erigeron flagellaris</i>	Gray
<i>Erigeron formosissimus</i>	Greene
<i>Erigeron neomexicanus</i>	Gray
<i>Erigeron speciosus</i>	(Lindl.) DC.
<i>Eriogonum alatum</i>	Torr.
<i>Eriogonum racemosum</i>	Nutt.
<i>Erodium cicutarium</i> *	(L.) L'Hér. ex Ait.
<i>Escobaria vivipara</i>	(Nutt.) Buxbaum
<i>Euphorbia</i> sp.	L.
<i>Fragaria vesca</i>	L.
<i>Frasera speciosa</i>	Dougl. ex Griseb.
<i>Galium aparine</i>	L.
<i>Galium wrightii</i>	Gray
<i>Gayophytum diffusum</i>	Torr. & Gray
<i>Geranium</i> sp.	L.
<i>Geranium caespitosum</i>	James
<i>Glandularia gooddingii</i>	(Briq.) Solbrig
<i>Hedeoma drummondii</i>	Benth.
<i>Hedeoma hyssopifolia</i>	Gray
<i>Heliomeris multiflora</i>	Nutt.
<i>Heterotheca villosa</i>	(Pursh) Shinnars

Species name	Authority
<i>Hieracium fendleri</i>	Schultz-Bip.
<i>Houstonia wrightii</i>	Gray
<i>Hymenopappus filifolius</i>	Hook.
<i>Hymenopappus mexicanus</i>	Gray
<i>Hymenothrix wrightii</i>	Gray
<i>Hymenoxys bigelovii</i>	(Gray) Parker
<i>Ipomoea costellata</i>	Torr.
<i>Ipomoea plummerae</i>	Gray
<i>Ipomopsis aggregata</i>	(Pursh) V. Grant
<i>Ipomopsis</i> sp.	Michx.
<i>Ipomopsis multiflora</i>	(Nutt.) V. Grant
<i>Iris missouriensis</i>	Nutt.
<i>Lactuca serriola</i> *	L.
<i>Lactuca tatarica</i>	(L.) C.A. Mey.
<i>Laennecia schiedeana</i>	(Less.) Nesom
<i>Lathyrus</i> sp.	L.
<i>Lathyrus lanszwertii</i>	Kellogg
<i>Lathyrus lanszwertii</i> var. <i>leucanthus</i>	Kellogg
<i>Lathyrus laetivirens</i>	Greene ex Rybd.
<i>Leibnitzia lyrata</i>	(D. Don) G.L. Nesom
<i>Lepidium densiflorum</i>	Schrad.
<i>Linum lewisii</i>	Pursh
<i>Linum neomexicanum</i>	Greene
<i>Linum</i> sp.	L.
<i>Lithospermum cobrense</i>	Greene
<i>Lithospermum</i> sp.	L.
<i>Lithospermum incisum</i>	Lehm.
<i>Lithospermum multiflorum</i>	Torr. ex Gray
<i>Lotus</i> sp.	L.
<i>Lotus wrightii</i>	(Gray) Greene
<i>Lupinus hillii</i>	Greene
<i>Machaeranthera canescens</i>	(Pursh) Gray
<i>Machaeranthera gracilis</i>	(Nutt.) Shinnars
<i>Malaxis soulei</i>	L.O. Williams
<i>Malva neglecta</i> *	Wallr.
<i>Medicago lupulina</i> *	L.
<i>Melilotus officinalis</i> *	(L.) Lam.
<i>Microsteris gracilis</i>	(Hook.) Greene
<i>Mirabilis decipiens</i>	(Standl.) Standl.
<i>Mirabilis linearis</i>	(Pursh) Heimerl.
<i>Mirabilis multiflora</i>	(Torr.) Gray

Species name	Authority
<i>Monarda fistulosa</i> ssp. <i>fistulosa</i> var. <i>menthifolia</i>	L.
<i>Monotropa hypopithys</i>	L.
<i>Nama dichotomum</i>	(Ruiz & Pavón) Choisy
<i>Navarretia</i> sp.	Ruiz & Pav.
<i>Noccaea montana</i>	(L.) F.K. Mey.
<i>Oenothera albicaulis</i>	Pursh
<i>Oenothera coronopifolia</i>	Torr. & Gray
<i>Oenothera elata</i>	Kunth
<i>Oenothera pubescens</i>	Willd. ex Spreng.
<i>Onopordum acanthium</i> *	L.
<i>Opuntia</i> sp.	P. Mill.
<i>Oxalis</i> sp.	L.
<i>Packera multilobata</i>	(Torr. & Gray ex Gray) W.A. Weber & A. Löve
<i>Packera neomexicana</i>	(Gray) W.A. Weber & A. Löve
<i>Pedicularis centranthera</i>	Gray
<i>Pennellia longifolia</i>	(Benth.) Rollins
<i>Penstemon barbatus</i>	(Cav.) Roth
<i>Penstemon linarioides</i>	Gray
<i>Penstemon pachyphyllus</i>	Gray ex Rydb.
<i>Penstemon</i> sp.	Schmidel
<i>Penstemon virgatus</i>	Gray
<i>Phacelia</i> sp.	Juss.
<i>Phacelia egena</i>	(Greene ex Brand) Greene ex J.T. Howell
<i>Phacelia heterophylla</i>	Pursh
<i>Phaseolus angustissimus</i>	Gray
<i>Phaseolus grayanus</i>	Woot. & Stadl.
<i>Physalis hederifolia</i>	Gray
<i>Plantago argyraea</i>	Morris
<i>Polygala alba</i>	Nutt.
<i>Polygala obscura</i>	Benth.
<i>Polygonum aviculare</i> *	L.
<i>Polygonum douglasii</i>	Greene
<i>Portulaca oleracea</i>	L.
<i>Potentilla</i> sp.	L.
<i>Potentilla hippiana</i>	Lehm.
<i>Potentilla norvegica</i>	L.
<i>Potentilla thurberi</i>	Gray
<i>Prunella vulgaris</i>	L.
<i>Pseudocymopterus montanus</i>	(Gray) Coult. & Rose
<i>Pseudognaphalium canescens</i>	(DC.) W.A. Weber
<i>Pseudognaphalium macounii</i>	(Greene) Kartesz

Species name	Authority
<i>Psoralidium tenuiflorum</i>	(Pursh) Rydb.
<i>Pteridium aquilinum</i>	(L.) Kuhn
<i>Pterospora andromedea</i>	Nutt.
<i>Rudbeckia hirta</i>	L.
<i>Rumex acetosella</i> *	L.
<i>Rumex crispus</i> *	L.
<i>Sanguisorba minor</i> *	Scop.
<i>Saxifraga rhomboidea</i>	Greene
<i>Schoenocrambe linearifolia</i>	(Gray) Rollins
<i>Senecio wootonii</i>	Greene
<i>Silene lacinata</i>	Cav.
<i>Solanum americanum</i>	P. Mill.
<i>Solidago sp.</i>	L.
<i>Solidago missouriensis</i>	Nutt.
<i>Solidago velutina</i>	DC.
<i>Sphaeralcea sp.</i>	St.-Hil.
<i>Stevia plummerae</i>	Gray
<i>Stevia serrate</i>	Cav.
<i>Symphyotrichum falcatum</i>	(Lindl.) Nesom.
<i>Taraxacum officinale</i> *	G.H.Weber ex Wiggers
<i>Tetraneuris acaulis</i>	(Pursh) Greene
<i>Tetraneuris argentea</i>	(Gray) Greene
<i>Tetraneuris ivesiana</i>	Greene
<i>Thalictrum fendleri</i>	Engelm. ex Gray
<i>Thermopsis montana var. montana</i>	Nutt.
<i>Townsendia exscapa</i>	(Richards.) Porter
<i>Toxicodendron rydbergii</i>	(Small ex Rydb.) Greene
<i>Tradescantia pinetorum</i>	Greene
<i>Tragia ramosa</i>	Torr.
<i>Tragopogon dubius</i> *	Scop.
<i>Trifolium sp.</i>	L.
<i>Valeriana arizonica</i>	Gray
<i>Verbascum thapsus</i> *	L.
<i>Verbena bracteata</i>	Cav. ex Lag. & Rodr.
<i>Veronica anagallis-aquatica</i>	L.
<i>Vicia americana</i>	Muhl. ex Willd.
<i>Vicia pulchella</i>	Kunth
<i>Vitis arizonica</i>	Engelm.
<i>Wyethia arizonica</i>	Gray

Graminoids

<i>Achnatherum nelsonii</i>	(Scribn.) Barkworth
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Species name	Authority
<i>Agropyron desertorum</i> *	(Fisch. ex Link) J.A. Schultes
<i>Agrostis scabra</i>	Willd.
<i>Aristida arizonica</i>	Vasey
<i>Aristida purpurea</i>	Nutt.
<i>Aristida schiedeana</i> var. <i>orcuttiana</i>	Trin. & Rupr.
<i>Blepharoneuron tricholepis</i>	(Torr.) Nash
<i>Bouteloua curtipendula</i>	(Michx.) Torr.
<i>Bouteloua gracilis</i>	(Willd. ex Kunth) Lag. ex Griffiths
<i>Bouteloua</i> sp.	Lag.
<i>Bromus carinatus</i>	Hook. & Arn.
<i>Bromus ciliatus</i>	L.
<i>Bromus japonicus</i> *	Thunb.
<i>Bromus tectorum</i> *	L.
<i>Carex</i> sp.	L.
<i>Carex geophila</i>	Mackenzie
<i>Carex leucodonta</i>	T. Holm
<i>Cyperus</i> sp.	L.
<i>Cyperus fendlerianus</i>	Boeckl.
<i>Cyperus niger</i>	Ruiz & Pav.
<i>Dactylis glomerata</i> *	L.
<i>Danthonia californica</i>	Boland.
<i>Dichanthelium oligosanthos</i>	(J. A. Schultes) Gould
<i>Echinochloa crus-galli</i> *	(L.) Beauv.
<i>Eleocharis macrostachya</i>	Britton.
<i>Elymus elymoides</i>	(Raf.) Swezey
<i>Elymus trachycaulus</i>	(Link) Gould ex Shinnars
<i>Eragrostis curvula</i> *	(Schrud.) Nees
<i>Eragrostis</i> sp.	von Wolf
<i>Festuca arizonica</i>	Vasey
<i>Hesperostipa comata</i>	(Trin. & Rupr.) Barkworth
<i>Juncus ensifolius</i>	Wikstr.
<i>Koeleria macrantha</i>	(Ledeb.) J.A. Schultes
<i>Lycurus phleoides</i>	Kunth
<i>Muhlenbergia</i> sp.	Schreb.
<i>Muhlenbergia longiligula</i>	A.S. Hitchc.
<i>Muhlenbergia minutissima</i>	(Steud.) Swallen
<i>Muhlenbergia montana</i>	(Nutt.) A.S. Hitchc.
<i>Muhlenbergia rigens</i>	(Benth.) A.S. Hitchc.
<i>Muhlenbergia virescens</i>	(Kunth) Kunth
<i>Nassella viridula</i>	(Trin.) Barkworth
<i>Panicum</i> sp.	L.
<i>Panicum bulbosum</i>	Kunth

Species name	Authority
<i>Panicum virgatum</i>	L.
<i>Pascopyrum smithii</i>	(Rydb.) A. Löve
<i>Piptochaetium pringlei</i>	(Beal) Parodi
<i>Poa compressa</i> *	L.
<i>Poa fendleriana</i>	(Steud.) Vasey
<i>Poa pratensis</i> *	L.
<i>Schizachyrium scoparium</i>	(Michx.) Nash
<i>Setaria viridis</i> *	(L.) Beauv.
<i>Sporobolus cryptandrus</i>	(Torr.) Gray
<i>Sporobolus interruptus</i>	Vasey
<i>Sporobolus sp.</i>	R. Br.