

THESIS

UNDERSTORY COMMUNITY DYNAMICS TEN YEARS AFTER A MIXED-SEVERITY
WILDFIRE IN PONDEROSA PINE AND ASPEN STANDS IN THE BLACK HILLS OF
SOUTH DAKOTA, USA.

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ABSTRACT

UNDERSTORY COMMUNITY DYNAMICS TEN YEARS AFTER A MIXED-SEVERITY WILDFIRE IN PONDEROSA PINE AND ASPEN STANDS IN THE BLACK HILLS OF SOUTH DAKOTA, USA.

Wildfires are important disturbances due to their ability to influence many ecosystem processes and functions. Following a mixed-severity wildfire, understory vegetation composition and structure may undergo both long- and short-term changes because of modified growing conditions, removal of overstory competition and changes in the amounts of available resources. While more rapid, short-term changes are easily observed and documented, understanding long-term changes is of critical importance for management purposes and allowing professionals to gain insights into forest composition following a major disturbance. Late in the summer of 2000, 34,000 ha of ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests in the Black Hills of South Dakota burned in what is now called the Jasper Fire; the largest wildfire recorded in the state's history. The Jasper Fire was classified as a mixed-severity wildfire resulting in a mosaic of areas burned at low- (25%), moderate- (48%) and high-severity (27%). Following the fire, plant communities appeared to recover rapidly leading to questions regarding how long various postfire communities would persist, how postfire community development varied by fire severity, and differences observed between zones of the Jasper Fire. Ultimately, many were interested in long-term postfire community dynamics. In this study we examined the understory vegetation composition and structure (relative abundance of graminoids, forbs and shrubs) and frequency of invasive species relative to fire severity (unburned, low, moderate and high) and zone (northern, central and southern) in ponderosa pine

and aspen (*Populus tremuloides* Michx.) stands 10 years after the Jasper Fire in the Black Hills of South Dakota, USA. In both ponderosa pine and aspen sites, understory community composition differed by zone and severity simultaneously. In ponderosa pine stands, canopy cover of four species varied by only zone or severity and eleven varied by zone and severity simultaneously. In aspen stands, canopy cover of two species varied only by zone or severity and canopy cover of three species varied by zone and severity simultaneously. Grass and shrub cover were explained by the interaction of zone and severity in ponderosa pine stands while cover of forbs varied by zone and severity but not their interaction. In aspen stands grass, forb and shrub cover all varied by zone and severity simultaneously. Grass and forb cover values 10 years postfire were similar to the 5 year postfire levels, and were greatest in moderate and high-severity burned areas. Shrub cover was also similar 5 and 10 years postfire, with lower values in burned areas driven by the loss of common juniper (*Juniperus communis* L.). Although common juniper cover was drastically decreased by fire, other shrubs are beginning to appear across the landscape. Total plant cover appeared to be lower 10 years postfire than compared to 5 years postfire which might be driven by a shift from annual and biennial plants to perennial plants. Frequencies of invasive species reached 60-70%, however, canopy cover of individual invasive species never exceeded 5% in either ponderosa pine or aspen stands. Ten years postfire, burned areas support understory plant communities dominated by native perennial plants with very few invasive exotic species. Post-fire rehabilitation efforts need to be designed on a site-specific basis and invasive species monitoring should continue to ensure that these plants do not become a concern in the future.

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TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS	iv
INTRODUCTION	1
METHODS	9
<i>Study Area</i>	9
<i>Experimental Design</i>	9
<i>Understory Measurements</i>	11
<i>Data Analysis</i>	13
RESULTS	16
<i>Ponderosa</i>	16
<i>Aspen</i>	27
DISCUSSION	34
CONCLUSIONS & MANAGEMENT IMPLICATIONS	54
LITERATURE CITED	58
APPENDICES	66
<i>Appendix 1</i>	66

Appendix 2 72

Appendix 3 73

Appendix 4 74

Appendix 5 82

Appendix 6 83

LIST OF TABLES

Table 1. Comparison of species composition based on canopy cover of understory plants ($\alpha = 0.10$) in ponderosa pine study sites from 3 zones (northern, central, and southern) and 4 fire severities (unburned, low, moderate and high) using a multi-response permutation procedure (MRPP). The chance corrected within-group homogeneity (A) is presented along with the p-value (P) associated with the A test statistic from the MRPP 17

Table 2. Comparison of species composition based on canopy cover of understory plants ($\alpha = 0.10$) grouped by burn severity (unburned, low, moderate, and high) in ponderosa pine study sites using a multi-response permutation procedure (MRPP). The chance corrected within-group homogeneity (A) is presented along with the p-value (P) associated with the A test statistic from the MRPP 17

Table 3. Results of ANOVA and indicator species analysis conducted on sampling categories and species of interest, in ponderosa pine stands, when comparing community composition between severity and zones. ANOVA was used to investigate the effects of fire severity and zone on canopy cover of indicator species, other species of interest, bare ground, litter and rock. Species of interest were selected based on field observations and indicator species had observed indicator values $\geq 50\%$ and P-values ≤ 0.05 in Monte Carlo test of significance using an indicator species analysis 18

Table 4. Percent canopy cover (means with SE in parentheses, n=12) of indicator species and species of interest in the ponderosa pine stands with zone main effects..... 19

Table 5. Percent canopy cover (means with SE in parentheses, n=9) of indicator species, species of interest and bare ground in the Ponderosa pine sites as affected by fire severity 20

Table 6. Percent canopy cover (means with SE in parentheses, n=3) for indicator species, species of interest and rock as affected by zone and severity interactions at ponderosa pine study sites 22

Table 7. Percent canopy cover (means with SE in parentheses, n=3) for functional groups (grasses, forbs and shrubs) and all plants combined (total) as affected by zone, severity and the two factors simultaneously at ponderosa pine study sites on the Black Hills National Forest..... 24

Table 8. Frequency (% , means with SE in parentheses, n=3) of invasive species as affected by fire severity in the ponderosa pine study sites 25

Table 9. Comparison of species composition based on canopy cover of understory plants ($\alpha = 0.10$) in aspen study sites from 2 zones (northern and central) and 3 fire severities (unburned, low and high) using a multi-response permutation procedure (MRPP). The chance corrected within-

group homogeneity (A) is presented along with the p-value (P) associated with the A test statistic from the MRPP 27

Table 10. Comparison of species composition based on canopy cover of understory plants ($\alpha = 0.10$) grouped by burn severity (unburned, low and high) in Aspen study sites using a multi-response permutation procedure (MRPP). The chance corrected within-group homogeneity (A) is presented along with the p-value (P) associated with the A test statistic from the MRPP 27

Table 11. Results of ANOVA and indicator species analysis conducted on sampling categories and species of interest, in aspen stands, when comparing community composition between severity and zones. ANOVA was used to investigate the effects of fire severity and zone on canopy cover of indicator species, other species of interest, bare ground, litter and rock. Species of interest were selected based on field observations and indicator species had observed indicator values $\geq 50\%$ and P-values ≤ 0.05 in Monte Carlo test of significance using an indicator species analysis 28

Table 12. Percent canopy cover (means with SE in parentheses, n=9) of indicator species and species of interest in the aspen stands with zone main effects 30

Table 13. Percent canopy cover (means with SE in parentheses, n=6) of indicator species and species of interest in the aspen sites as affected by fire severity 30

Table 14. Percent canopy cover (means with SE in parentheses, n=3) for functional groups affected by zone and severity interactions at aspen study sites 31

LIST OF FIGURES

Figure 1. The location, size and burn severities of the 2000 Jasper Fire (modified from Lentile et al. (2006) and Paleo Research Institute 2010)).....	10
Figure 2. Extended Daubenmire Frame (Bonham et al. 2004).....	13
Figure 3. Cover of exotic and invasive species by severity in ponderosa pine sites ten years postfire.....	26
Figure 4. Frequency of invasive species by severity in aspen sites ten years postfire	33
Figure 5. Cover of exotic and invasive species by severity in aspen sites ten years postfire	33

INTRODUCTION

Wildfires are important disturbances that influence many processes and functions in forested ecosystems (Agee 1993, Bond and Van Wilgen 1996). Keyser (2007 and citations within) points out that while fires are often viewed as catastrophic events, mixed-severity wildfires can increase understory heterogeneity by reducing fire-intolerant species and altering growing conditions. Subsequently, tree mortality may increase after fire which reduces competition for resources and allows the understory vegetation increased opportunities for growth (Hale 2003, Reigel et al. 1995). Because fire behavior is often variable in ponderosa pine forests, understory responses can be complex and trajectories of postfire understory community development may not become evident for many years. In this thesis, understory community composition was quantified and analyzed to study the effects of fire severity and location (zone) ten years after the Jasper Fire in the Black Hills of South Dakota.

Following a highly variable fire, the community structure and dynamics of understory vegetation can also be highly variable and the overall community development may not become evident until many years after the event. Factors such as fire severity, intensity, seasonality, and periodicity (Wright and Bailey 1982) along with precipitation events (Anderson et al. 1968, Moore et al. 2006) all influence the nature of change and re-growth of understory vegetation following a fire. Fire severity drives postfire conditions and greatly influences understory re-growth (Bataineh et al. 2006). Two and 4 years after the Rattle Burn Fire, Bataineh et al. (2006) found areas that burned under low and high-severities showed little to no differences compared to unburned areas but after 30 years they observed differences between the low and high-severity sites. Overstory structural damage is sometimes not immediate following a fire (Keyser et al.

2006, Agee 2003, Ryan et al. 1988) prolonging opportunities for understory re-growth. These findings suggest that long-term data collection is beneficial for studying and understanding understory community dynamics following a mixed-severity fire.

Changes in relative abundances of functional groups and individual species are of interest when investigating community dynamics. Presence of invasive plants is also of immense concern following a disturbance like the Jasper Fire. Non-native plants often out-compete native species (Griffis 2001) and many investigators document increased abundances of exotic plants following fires (Zedler and Scheid 1988, Crawford et al. 2001, Hunter et al. 2006, Gundale et al. 2006, etc.). Because most problematic invasive plants are exotic, documentation of presence and absence of these species is very important. In ponderosa pine ecosystems, there are few records of the establishment and life cycles of non-native species (Keyser 2007). Therefore, documentation of presence or absence of these species is critical for determining management strategies and understanding the role these species play in the Black Hills environment following a disturbance of this magnitude.

While overstory regrowth of aspen stands following fire has been fairly well documented (Bartos and Mueggler 1981; Keyser et al. 2005; Kay 1993; Romme et al. 1997; etc.) there is far less information regarding understory community dynamics and recovery. Responses of aspen stands to fire are quite unique in that aspen regenerate vigorously using both sexual and vegetative means following fire (Hessl and Graumlich 2002). Aspen stands have fairly short life spans (Kaye et al. 2003) and are moderately dependent on the occurrence of fire to persist and expand instead of being out-competed by other trees (Keyser et al. 2005). Changes to aspen overstory in the Black Hills might lead to significant changes in the understory communities found in these stands, which could affect the composition of the entire forest. Keyser et al.

(2005) pointed out that numerous professionals believe aspen stands in the west might actually be at risk of being replaced by less diverse conifer-dominated forests. It is believed that the short life span of aspen, decreases in aspen vigor and abundance and other factors drive the loss of aspen (Keyser et al. 2005). Studying the understory community dynamics in aspen stands will help to answer questions concerning long-term changes of aspen communities in the Black Hills and provide increased documentation of aspen understory responses to fire.

There is an unmet need for further research leading to an improved understanding of large, mixed-severity fires and the responses of vegetation to these fires. Lentile et al. (2005) emphasize this point when stating that mixed-severity fire regimes were the most complex and least understood in the western part of the U.S. Over the last century, few large-scale mixed-severity fires have occurred in ponderosa pine forests mainly due to manipulation of forests and management strategies (Arno et al. 2000) which have limited opportunities for researchers to study these fires and the response of vegetation to them. Many studies were conducted on the Jasper Fire in South Dakota providing a plethora of information about mixed-severity fire in ponderosa pine forests (Bonnet et al. 2004; Bonnet et al. 2005; Keyser et al. 2005; Keyser et al. 2006; Keyser et al. 2008; Keyser et al. 2009; Lentile et al. 2005; and Lentile et al. 2006) while similar studies elsewhere concerning the two (ponderosa pine and mixed-severity fire) are limited. Other studies focus on and provide excellent information about effects of prescribed burn treatments specifically in ponderosa pine forests. Some studies have investigated mixed-severity fire effects in several forest types and others have investigated understory responses to mainly prescribed fire in ponderosa pine forests. While these studies provide information about possible responses of ponderosa pine forests to fire, mixed-severity fire regimes and understory

responses they provide at best, a piecemeal characterization of ponderosa pine overstory and understory responses to mixed-severity wildfire.

Many studies have investigated the effects of prescribed burning on ponderosa pine forests. Harrington (1987) investigated the effects of crown scorching on ponderosa pine mortality in different seasons from prescribed burns in the San Juan National Forest in Colorado. Tree mortality caused by prescribed fire during the fall season in ponderosa pine forests along the Colorado Front Range was investigated by Wyant et al. (1986) and a similar study investigated potential accelerated mortality of large ponderosa pines due to prescribed burning at Crater Lake National Park (Swezy and Agee 1990). McHugh and Kolb (2003) also assessed tree mortality from fire but looked at both wild and prescribed fires in ponderosa pine forests. These studies provide information regarding ponderosa pine responses to fire but they do not necessarily provide an indication of how ponderosa pine forests respond to large, mixed-severity wildfires.

Low- and high-severity fire regimes and fire effects are quite common and conceptually easy to understand because of fairly uniform conditions. Mixed-severity fires are highly variable in nature and not well understood nor documented (Fulè et al. 2003 and Perry et al. 2011). Arno et al. (2000), who looked at forests where mixed-severity fire regimes once dominated, discussed effects of management and fire suppression and offered possible management actions that might be used to return these forests to a historical mixed-severity fire regime. Thompson and Spies (2010) examined patterns of crown damage following recurring mixed-severity fires in an area dominated by conifer species in southwestern Oregon while Fornwalt et al. (2010) examined the influence of a mixed-severity wildfire (Hayman Fire) on exotic plants in a ponderosa pine forest in Colorado. Hayes and Robeson (2011) examined the relationship between fire severity and

landscape-pattern following a mixed-severity fire in New Mexico. Although these studies provide valuable information on mixed-severity fire effects, not one of them specifically encompasses both understory and overstory vegetation effects in ponderosa pine forests.

The responses of understory vegetation in ponderosa pine forests following a fire have been documented but mostly following prescribed burns and not wildfires. Armour et al. (1984) investigated the effects of differing fire intensities following prescribed burns on understory vegetation in ponderosa pine forests and a similar study by Kerns et al. (2006) investigated herbaceous richness and cover in response to season and severity of prescribed burning in ponderosa pine forests in Oregon. Griffis et al. (2001) broadened the scope and examined understory responses to not only prescribed burning but also areas that were burned by stand-replacing wildfire in ponderosa pine forests of northern Arizona. These studies provide an indication of understory community dynamics in ponderosa pine forests following fire but the effects of mixed-severity wildfires are not well documented.

A number of studies have been conducted on the responses of ponderosa pine forests to prescribed fire, mixed-severity fire effects on different forest types and several on understory responses to fire. On the other hand, there are very few studies on understory responses to mixed-severity fire in ponderosa pine forests and even fewer long-term studies. The lack of long-term studies of overstory and understory vegetation dynamics following mixed-severity fires highlights the importance and uniqueness of the studies conducted on the Jasper Fire. These studies offer guidance for making management decisions and help further the understanding of overstory and understory vegetation responses to mixed-severity fire in ponderosa pine forests.

Following the Jasper Fire, many studies were conducted to improve our understanding of overstory responses to mixed-severity fires in ponderosa pine forests and aspen stands of the Black Hills (Bonnet et al. 2004; Bonnet et al. 2005; Keyser et al. 2005; Keyser et al. 2006; Keyser et al. 2008; Keyser et al. 2009; Lentile et al. 2005; and Lentile et al. 2006). Keyser et al. (2009) evaluated the ecological effects of salvage activities implemented after the Jasper Fire by comparing salvaged and non-salvaged sites. Keyser et al. (2005) studied how fire impacts the expansion and persistence of small aspen clones in the Black Hills. Accurate models were developed to predict 5-year mortality of ponderosa pine using tree morphology and observed fire effects (Keyser et al. 2006). An evaluation of short-term effects of large, mixed-severity fire on ecological recovery was conducted by Keyser et al. (2007). Bonnet et al. (2004) characterized favorable and unfavorable environmental conditions for seedling establishment following the Jasper Fire. Effects of postfire environmental conditions on ponderosa pine regeneration were also studied (Bonnet et al. 2005). Another study examined relationships between burn severity, topography and pre-fire stand structure in large managed ponderosa pine forests to gain insight into forest conditions where severe fire effects are likely (Lentile et al. 2006). Lentile et al. (2005) examined fire effects such as fire-scars, patch structure and tree regeneration to determine: 1) relationships between fire-effects and burn severity; 2) fire history left by the Jasper Fire; and 3) relationships between historical fire regimes and indicators of fire effects in the Black Hills. Collectively, these studies provided a comprehensive description of forest overstory responses to the Jasper Fire, but did not provide information as to what was occurring in the understory of the Black Hills following the fire.

A study was conducted over the first five years following the Jasper Fire which analyzed changes in understory vegetation composition and structure (Keyser 2007). This study provided

a detailed characterization of rapid, short-term postfire changes following the Jasper Fire and highlighted the need for long-term characterizations of postfire understory succession following mixed-severity fires. The research described in this thesis was conducted specifically to address that need.

The overall goal of this study was to quantitatively describe understory plant communities present ten years after the mixed-severity Jasper Fire in ponderosa pine and aspen ecosystems to gain better insight into postfire succession. The objectives of this study were to: 1) compare native species composition, and functional group composition of ponderosa pine and aspen sites as affected by fire severity in the northern, central and southern zones of the Jasper Fire, and 2) quantify the occurrence and distribution of invasive plants as affected by fire severity in the northern, central and southern zones of the Jasper Fire. The hypotheses of this study were:

- Shrubs will have the greatest canopy cover in the unburned and low-severity burn areas, specifically, common juniper will not be present in the moderate and high-severity burns 10 years post fire.
- Non-native species will have the greatest frequency in the moderate and high-severity burn areas.
- Canopy cover of individual exotic species will not exceed 10% in either the ponderosa pine or aspen sites.
- Grasses will be the most dominant of the functional groups and will have the greatest canopy cover in the low and moderate-severity burn areas.
- Some individual plant species and functional group responses to fire severity will vary by zone.

- Forb and shrub functional groups will have greater canopy cover in the northern and central zones compared to the southern zone, while canopy cover of grasses will be consistent across all 3 zones.
- Common juniper will only be present in the northern and southern zones and only in the unburned and low-severity sites.

The information gained from this study will help improve our understanding of long-term understory responses to mixed-severity wildfire in ponderosa pine and aspen systems in the Black Hills of South Dakota.

METHODS

Study Area

The study was located in the interior forests of the Black Hills National Forest (BHNF) of South Dakota, specifically inside the perimeter of the Jasper Fire. The Black Hills National Forest is dominated by ponderosa pine overstory with sparse understory vegetation interspersed with aspen and meadows (Lentile et al. 2006). The Black Hills are characterized as an isolated, forested uplift that ranges in elevation from 1800 – 2200 m (Bonnet et al. 2005). The climate of this region is continental with cold winters and mild, moist summers (Johnson 1949). Mean maximum and minimum daily temperatures range from -3.3°C in the winter to 13.2°C in the summer (Keyser et al. 2008). Annual precipitation averages 45 to 48 cm with approximately 65 – 75% of precipitation falling from April through October (Keyser et al. 2008). Dominant soil types are similar throughout the region including the study area and consist of Alfisols, Mollisols, and Inceptisols (Shepperd and Battaglia 2002).

The Jasper Fire was a mixed-severity fire that burned 34,000 ha of ponderosa pine forests and aspen stands in the BHNF over a 16-day period starting on August 24th, 2000 (US Forest Service 2000). The fire occurred at elevations between 1,500 and 2,100 m (Keyser et al. 2006). A combination of surface fire, passive crown fire, and active crown fire all occurred (US Forest Service 2000). Lentile et al. (2006) explained that the Jasper Fire was 25% larger than any other fire ever recorded in the Black Hills and consumed a total of 7% of the Limestone Plateau.

Experimental Design

This study was designed to characterize the 10-year postfire understory vegetation by collecting data from plots established in earlier studies (Keyser 2007). The Jasper Fire was divided into three zones; northern, central, and southern. These zones were established because the fire burned in a north to south direction through elevation and precipitation gradients that also exist from north to south in the Black Hills (Keyser et al. 2006). In June of 2001 following

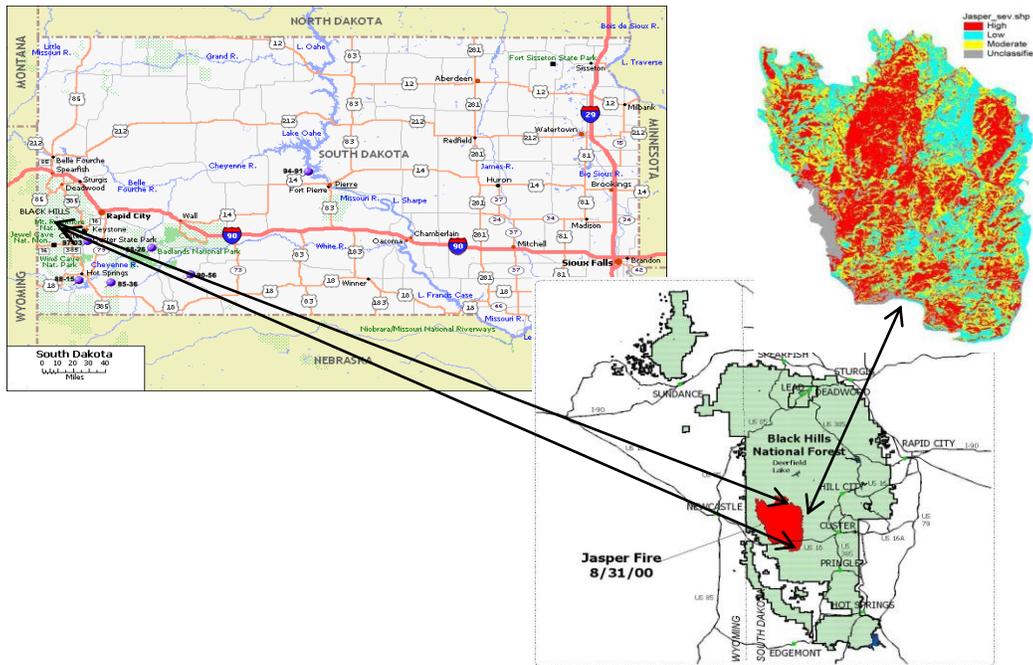


Figure 1. Location, size, and burn severities of the 2000 Jasper Fire (Figure modified from Lentile et al. (2006) and PaleoResearch Institute (2010)).

the Jasper Fire, three 800-ha forest units, one in each zone, were set aside so that long-term studies could be conducted in the three zones where no silvicultural activities would occur (Keyser et al. 2008). Within these three zones, 36 0.3-ha permanent ponderosa pine study sites were randomly located. Twenty-seven study sites were established inside the fire boundary and 9 directly outside of the boundary (Keyser et al. 2008). Throughout the study area, sites were established in four different burn severities: unburned, low, moderate and high. The 36 sites were established so that there would be 3 replicate sites in each burn severity in each zone. Nine

sites were located in stands where trees were estimated to have <25% crown fire damage and were designated as low-severity treatments. Nine sites were located in stands estimated to have >25% but <100% total crown damage and were designated as moderate-severity treatments. Nine sites were located in stands where 100% crown consumption occurred and were designated as high-severity treatments (Keyser et al. 2008). The remaining nine sites were located in unburned ponderosa pine stands and were used as the control (baseline) sites (Keyser et al. 2008).

Aspen stands were also studied to determine post fire vegetation dynamics. Eighteen aspen study sites were established with 12 burned sites and 6 sites directly outside the fire boundary. Aspen stands were only present in the northern and central zones in areas that burned at high and low severities. Severity was determined based on visual field inspections (Lentile et al. 2005 and Keyser et al. 2005). Six sites were located in aspen stands that had overstory mortality between 25% and 75% and were classified as low-severity fire treatments (Keyser et al. 2005). An additional 6 sites were located in stands with >75% aspen mortality and were classified as high-severity fire treatments (Keyser et al. 2005). The final 6 aspen sites were located in unburned aspen stands and were used as the control (baseline) sites. In the northern and central zones, 3 replicate sites of each fire severity (baseline, high and low) were randomly established, resulting in a total of 9 sites in each zone.

Understory Measurements

Plant canopy cover data were gathered on ponderosa pine and aspen study sites. Plant cover was used because it is recognized as an effective means for describing plant communities, describing plant-environment interactions, and for monitoring plant communities through time

(Bonham et al. 2004). Plant cover was also used to keep the measurements similar to those conducted by Keyser (2007) 1- and 5- years postfire.

The center of each study site was located in 2010 using GPS coordinates and the stakes originally used to mark each site in 2001. From the center point, 30-meter transects were established in the 4 cardinal directions. Once the transects were established, canopy cover by species and by functional group (graminoids, forbs and shrubs) was estimated using an extended Daubenmire frame measuring 50 x 100 cm (Bonham et al. 2004) (Figure 2). The frame consisted of five contiguous 20 x 50 cm Daubenmire frames which aids in reducing most sources of error when visually estimating plant cover (Bonham et al. 2004). Canopy cover was estimated from plots located 10, 20, and 30 meters from the plot center along each transect resulting in 12 sub-samples (frame locations) for each replicate (site). Each frame was positioned on the right side of the transect tape when facing outward from the plot center.

An extensive search for invasive species was conducted at each of the ponderosa pine and aspen sites. Observations of presence or absence of individual invasive plant species were collected to determine frequency. Invasive plants are highly competitive, persistent and are characterized as plants that can grow outside of their native habitat and cause harm to their new surrounding environment (USDA National Invasive Species Information Center 2011). Invasive plants of particular interest in the BHNF include Canada thistle (*Cirsium arvense* (L.) Scop.), houndstongue (*Cynoglossum officinale* L.), and leafy spurge (*Euphorbia esula* L.). Presence and absence was determined by establishing three, 0.03-ha, circular plots at compass bearings of 0°, 125°, and 225°. An extensive search of the area encompassed by a 20 meter diameter circle was conducted, looking closely at all vegetation and documenting the presence of all invasive plant species.

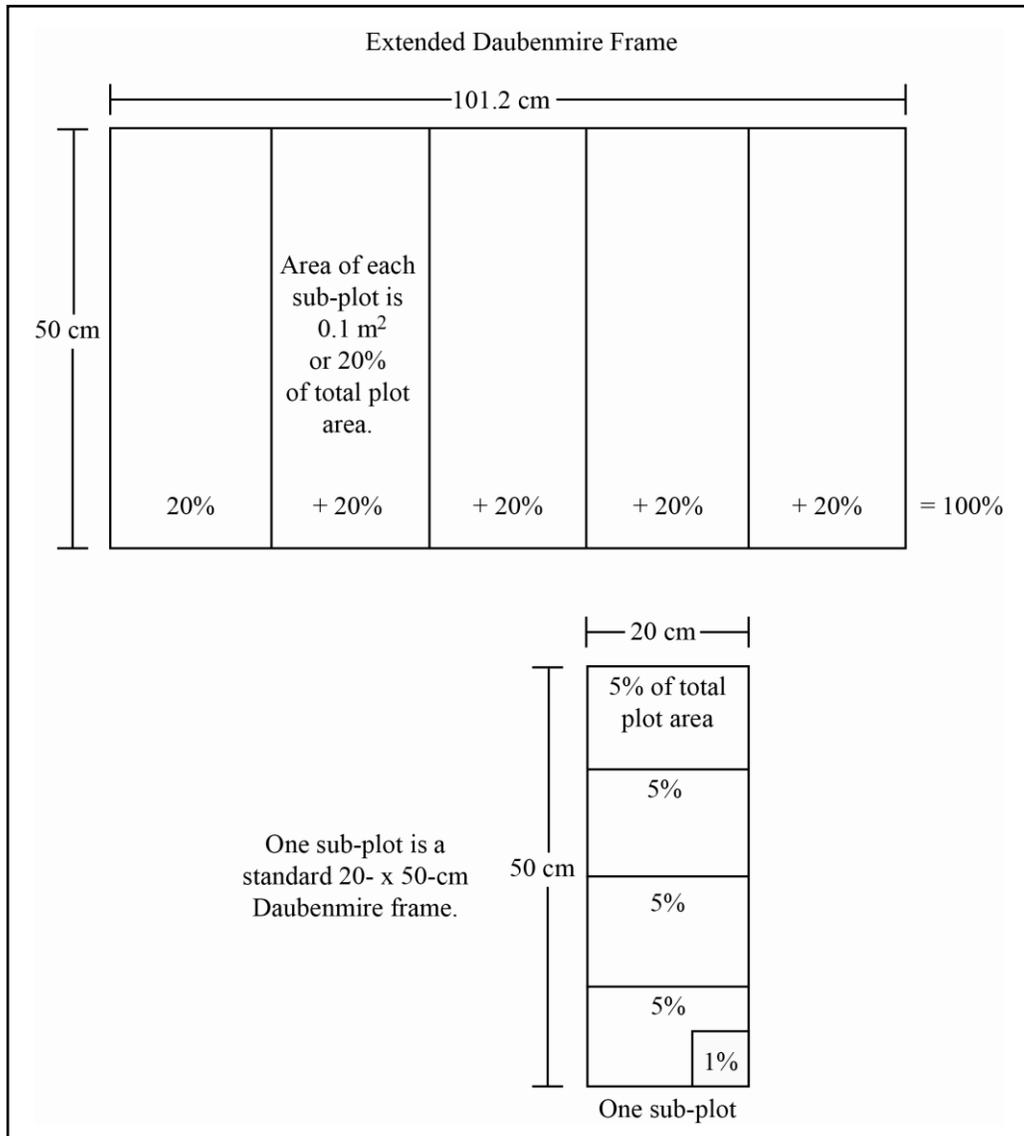


Figure 2. Extended Daubenmire Frame (Figure modified from Bonham et al. 2004).

Data Analysis

The primary comparisons of interest included potential differences in understory composition among burn severities in the three zones. A multi-response permutation procedure (MRPP) was conducted using PC-ORD Version 6 (McCune and Mefford 2011) to test for differences in species composition among zones and severities. This test is similar to multivariate analysis of variance in that it is a non-parametric analysis but it does not require

assumptions of multivariate normality and homogeneity of variances that are seldom met with ecological community data (McCune and Grace 2002) making it an appropriate fit for our analysis. The statistic *A* is a descriptor of within-group homogeneity compared to the random expectation and is known as the chance-corrected within-group agreement (McCune and Grace 2002). When species composition is identical between sites, the *A* statistic will equal 1 but if heterogeneity is random within groups, then the *A* statistic will be 0 (McCune and Grace 2002). If there is less agreement within groups than expected by chance, the *A* statistic will be < 0 (McCune and Grace 2002).

Indicator species analysis in PC-ORD Version 6 (McCune and Mefford 2011) using Dufrene and Legendre's (1997) method was used to determine which plants were likely driving community differences detected using MRPP. McCune and Grace (2002) explain that the indicator species analysis calculates the relative abundance (cover or biomass) of individual species at a particular site and the relative frequency of individual species which are then multiplied together and then by 100 to produce the indicator value. A high indicator value requires simultaneously high relative abundance and relative frequency. If either value is low for a particular species that species is determined to be a poor indicator (McCune and Grace 2002). Indicator values range from zero (no indication) to 100 (perfect indication) which means that presence of a species points to a particular group (McCune and Grace 2002). This test is often used in conjunction with the MRPP test to help explain species composition differences (McCune and Mefford 2002). The statistical significance of each indicator value is based on a Monte Carlo test and significance is based on 1000 permutations (McCune and Grace 2002). Plants with indicator values of 50 or greater and a p -value < 0.1 were analyzed further using analysis of variance.

Visual assessments of relationships between plant species abundance, zones and severities were made using nonmetric multidimensional scaling (NMS) ordination. Because ecological data often fails to meet assumptions of parametric tests, NMS is commonly recommended (Clarke 1993). Lee (2004) describes NMS as an analytical algorithm that iteratively seeks to position species (n) on dimensional axes (k) while minimizing the stress on the overall dimensional configuration.

Each indicator species and the other species of interest were then analyzed using analysis of variance (ANOVA) to determine the effects of fire severity and zone on canopy cover. Prior to running the ANOVA, percent cover data were square root transformed to meet the assumptions of the analysis. Mean separation tests were conducted using Tukey's method. Residual and normality plots were examined to confirm that assumptions of all analyses were met. Analysis of variance and pairwise mean comparisons were also used to determine the effects of fire severity and zone on frequency of exotic and invasive species, canopy cover of plant functional groups, and canopy cover of all plants combined (total plant cover). SAS 9.2 (2008) was used to perform all ANOVA's and associated mean separations. Tables and figures include non-transformed means and standard errors (original scale). The USDA Plants Database (2011) was used for all plant nomenclature.

RESULTS

Ponderosa

Plant species composition of understory communities in ponderosa pine stands differed simultaneously by zone and severity. With an MRPP analysis, the complex relationship between zone and severity is best examined by holding one factor constant and comparing levels of the other factor. All pairwise severity comparisons are organized by zone in Table 1. Table 2 compares communities associated with each severity across zones. Together, Tables 1 and 2 explain the interaction between severity and zone.

In all three zones, both the low- and moderate-severities differed from high-severity communities and the low- and moderate-severities were similar to one another (Table 1). In the northern zone, the unburned sites were different from all burn severities. In the central zone, burn areas could not be compared to unburned areas because one central unburned site was logged prior to data collection and had to be omitted (indicated by N/A in Tables 1 and 2). In the southern zone, low- and moderate-severity communities were similar to unburned communities but the high-severity communities differed from unburned sites (Table 1).

When ponderosa sites are organized by severity (Table 2) it becomes apparent that species composition of the unburned, low-, and moderate-severity sites in the northern zone differed from corresponding severities in the southern zone. The central unburned sites once again could not be compared to the other severities because one central unburned site had to be omitted. Species composition of low- and moderate-severity sites in the northern zone also differed from corresponding severities in the central zone. Low- and moderate-severity sites in the central and southern zones were similar. High-severity sites in the northern zone were

similar to high-severity sites in the central and southern zones, but the high-severity sites in the central zone differed from those in the southern zone (Table 2).

Table 1. Comparison of species composition based on canopy cover of understory plants ($\alpha = 0.10$) in ponderosa pine study sites from 3 zones (northern, central, and southern) and 4 fire severities (unburned, low, moderate and high) using a multi-response permutation procedure (MRPP). The chance corrected within-group homogeneity (A) is presented along with the p-value (P) associated with the A test statistic from the MRPP.

Severity Comparison	Northern Zone		Central Zone		Southern Zone	
	A	P	A	P	A	P
UNBURNED vs. LOW	0.13	0.026	0.27	N/A	0.087	0.11
UNBURNED vs. MOERATE	0.17	0.023	0.21	N/A	0.033	0.15
UNBURNED vs. HIGH	0.19	0.047	0.39	N/A	0.35	0.022
LOW vs. MODERATE	-0.057	0.70	0.039	0.18	0.038	0.22
LOW vs. HIGH	0.21	0.035	0.24	0.023	0.16	0.025
MODERATE vs. HIGH	0.17	0.040	0.19	0.026	0.28	0.022

Table 2. Comparison of species composition based on canopy cover of understory plants ($\alpha = 0.10$) grouped by burn severity (unburned, low, moderate, and high) in ponderosa pine study sites using a multi-response permutation procedure (MRPP). The chance corrected within-group homogeneity (A) is presented along with the p-value (P) associated with the A test statistic from the MRPP.

	A	P
UNBURNED		
NORTHERN ZONE vs. CENTRAL ZONE	0.39	N/A
NORTHERN ZONE vs. SOUTHERN ZONE	0.18	0.022
CENTRAL ZONE vs. SOUTHERN ZONE	0.26	N/A
LOW-SEVERITY		
NORTHERN ZONE vs. CENTRAL ZONE	0.27	0.022
NORTHERN ZONE vs. SOUTHERN ZONE	0.21	0.023
CENTRAL ZONE vs. SOUTHERN ZONE	0.057	0.17
MODERATE-SEVERITY		
NORTHERN ZONE vs. CENTRAL ZONE	0.19	0.023
NORTHERN ZONE vs. SOUTHERN ZONE	0.14	0.023
CENTRAL ZONE vs. SOUTHERN ZONE	0.037	0.15
HIGH-SEVERITY		
NORTHERN ZONE vs. CENTRAL ZONE	0.031	0.29
NORTHERN ZONE vs. SOUTHERN ZONE	0.062	0.12
CENTRAL ZONE vs. SOUTHERN ZONE	0.063	0.096

Indicator species analysis identified 9 plants likely contributing to differences in species composition revealed by the MRPP. These 9 species included bastard toadflax (*Comandra umbellata* (L.) Nutt.), hookedspur violet (*Viola adunca* Sm.), old man's whiskers (*Geum*

triflorum Pursh), roughleaf ricegrass (*Oryzopsis asperifolia* Michx.), hairystem gooseberry (*Ribes hirtellum* Michx.), sticky purple geranium (*Geranium viscosissimum* Fisch. & C.A. Mey. ex C.A. Mey), rock clematis (*Clematis columbiana* (Nutt.) Torr. & A. Gray var. *tenuiloba* (A. Gray) J. Pringle), heartleaf arnica (*Arnica cordifolia* Hook.) and strict blue-eyed grass (*Sisyrinchium montanum* Greene) (Table 3). Separate analyses of variance (ANOVA) were then conducted for each of those 9 species along with eight additional species of interest. The additional eight included flexile milkvetch (*Astragalus flexuosus* Douglas ex G. Don), arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.), creeping barberry (*Mahonia repens* (Lindl.) G. Don), Canada thistle (*Cirsium arvense* (L.) Scop.), northern bedstraw (*Galium boreale* L.), common juniper (*Juniperus communis* L.), Woods' rose (*Rosa woodsii* Lindl.) and western snowberry (*Symphoricarpos occidentalis* Hook.). Bare ground, litter, and rock were also of interest, so ANOVAs were conducted on these as well.

Out of the twenty ANOVAs, canopy cover of fifteen species varied by zone, severity or both factors simultaneously. Cover of creeping barberry, hookedspur violet and flexile milkvetch varied by zone. Creeping barberry was the only species for which cover differed only by zone ($P = <0.0001$). Hookedspur violet's cover differed by zone ($P = 0.0033$) but that response varied by severity ($P = 0.081$). Flexile milk vetch abundance also differed by severity ($P = 0.0002$) (Table 3).

Table 3. Results of ANOVA and indicator species analysis conducted on sampling categories and species of interest, in ponderosa pine stands, when comparing community composition between severity and zones. ANOVA was used to investigate the effects of fire severity and zone on canopy cover of indicator species, other species of interest, bare ground, litter and rock. Species of interest were selected based on field observations and indicator species had observed indicator values $\geq 50\%$ and p-values ≤ 0.1 in Monte Carlo test of significance using an indicator species analysis.

	ANALYSIS OF VARIANCE			INDICATOR SPECIES ANALYSIS	

Species ¹	Zone Main Effect (P)	Severity Main Effect (P)	Zone x Severity Interaction (P)	Indicator Value	P
flexile milkvetch	0.084 ²	0.0002	0.32	N/A	N/A
creeping barberry	<0.0001	0.29	0.61	N/A	N/A
bare ground	0.47	<0.0001	0.52	N/A	N/A
Canada thistle	0.13	0.0005	0.62	N/A	N/A
arrowleaf balsamroot	<0.0001	0.0074	0.0017	N/A	N/A
bastard toadflax	0.036	0.023	0.0080	67	0.059
common juniper	0.15	0.0009	0.094	N/A	N/A
heartleaf arnica	0.093	0.074	0.042	67	0.066
hookedspur violet	0.0033	0.28	0.081	56	0.024
northern bedstraw	0.072	0.51	0.080	N/A	N/A
old man's whiskers	0.11	0.078	0.0098	59	0.059
rock	0.52	<0.0001	0.074	N/A	N/A
sticky purple geranium	0.12	0.095	0.061	67	0.066
western snowberry	0.0003	0.10	0.0055	N/A	N/A
Woods' rose	0.38	0.037	0.0035	45	0.021
hairystem gooseberry	0.38	0.41	0.45	50	0.056
litter	0.34	0.32	0.53	N/A	N/A
rock clematis	0.45	0.37	0.13	53	0.065
roughleaf ricegrass	0.38	0.41	0.45	50	0.058
strict blue-eyed grass	0.23	0.23	0.21	67	0.052

¹Species of interest and sampling categories included: Arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.), bastard toadflax (*Comandra umbellata* (L.) Nutt), Canada thistle (*Cirsium arvense* (L.) Scop.), common Juniper (*Juniperus communis* L.), creeping barberry (*Mahonia repens* (Lindl.) G. Don), flexile milkvetch (*Astragalus flexuosus* Douglas ex G. Don), hairystem gooseberry (*Ribes hirtellum* Michx.), heartleaf arnica (*Arnica cordifolia* Hook.), hookedspur violet (*Viola adunca* Sm.), northern bedstraw (*Galium boreale* L.), old man's whiskers (*Geum triflorum* Pursh), rock clematis (*Clematis columbiana* (Nutt.) Torr. & A. Gray var. *tenuiloba* (A. Gray) J. Pringle), roughleaf ricegrass (*Oryzopsis asperifolia* Michx.), sticky purple geranium (*Geranium viscosissimum* Fisch. & C.A. Mey. ex C.A. Mey), strict blue-eyed grass (*Sisyrinchium montanum* Greene), western snowberry (*Symphoricarpos occidentalis* Hook.), Woods' rose (*Rosa woodsii* Lindl.), bare ground, litter, and rock.

²P-values for significant main effect and interaction terms appear in bold text, while un-bolded P-values indicate that a particular effect or the ANOVA model was insignificant.

Table 4 presents the main effect of zone on the abundance of creeping barberry and flexile milkvetch. Creeping barberry was most abundant in the northern zone. Flexile milkvetch was more abundant in the central zone than the southern zone.

Table 4. Percent canopy cover (means with SE in parentheses, n=12) of indicator species and species of interest in the ponderosa pine stands with zone main effects.

Species	Zone
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	Northern	Central	Southern
creeping barberry (SE)	7.7 ^A (1.3)	0.63 ^B (0.63)	0.014 ^B (0.014)
flexile milkvetch (SE)	1.7 ^{AB} (0.61)	2.5 ^A (0.70)	1.1 ^B (0.43)
Means in a row with the same letter are not different, Tukey's method, $\alpha = 0.10$. Species included: creeping barberry (<i>Mahonia repens</i> (Lindl.) G. Don) and flexile milkvetch (<i>Astragalus flexuosus</i> Douglas ex G. Don).			

The effects of severity on abundance of flexile milkvetch, Canada thistle and bare ground are presented in Table 5. Bare ground and flexile milkvetch cover were greatest in the high-severity sites, while Canada thistle cover was greatest in the moderate-severity sites.

Table 5. Percent canopy cover (means with SE in parentheses, n=9) of indicator species, species of interest and bare ground in the ponderosa pine sites as affected by fire severity.

Species	Burn Severity			
	Unburned	Low	Moderate	High
bare ground (SE)	0.30 ^B (0.16)	2.3 ^B (0.98)	2.3 ^B (1.2)	17 ^A (4.1)
Canada thistle (SE)	0.0093 ^B (0.0093)	1.2 ^B (0.83)	3.4 ^A (0.89)	0.89 ^B (0.34)
flexile milkvetch (SE)	0.37 ^B (0.19)	0.77 ^B (0.26)	1.6 ^B (0.54)	4.2 ^A (0.76)
Means in a row with the same letter are not different, Tukey's method, $\alpha = 0.10$. Species and categories included: Bare ground, Canada thistle (<i>Cirsium arvense</i> (L.) Scop.) and flexile milkvetch (<i>Astragalus flexuosus</i> Douglas ex G. Don).				

Cover of ten plant species and the rock category, varied simultaneously by zone and severity (Table 6). Heartleaf arnica (*Arnica cordifolia* Hook.) and sticky purple geranium (*Geranium viscosissimum* Fisch. & C.A. Mey. ex C.A. Mey.) were only present in the northern zone at low burn severity sites. Arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.) also occurred only in the northern zone, and had greater cover in low- and moderate-severity sites than unburned and high-severity sites (Table 6).

In the northern zone, Woods' rose (*Rosa woodsii* Lindl.) was more abundant in the high-severity sites than low- and moderate-severity sites, but no different from unburned sites. Woods rose was present in the central and southern zones but no differences were detected among severities (Table 6).

Western snowberry (*Symphoricarpos occidentalis* Hook.) cover was greater in high-severity sites than low-severity sites in the northern zone. In the central zone, western snowberry cover was greater in high-severity sites than unburned sites. In the southern zone, western snowberry cover was similar across fire severities (Table 6).

Common juniper (*Juniperus communis* L.) consistently disappeared with any type of fire in the northern and central zones. Very little common juniper was encountered in the southern zone, even in the unburned sites (Table 6).

Hookedspur violet cover was consistent across all fire severities in the northern and southern zones. In the central zone, cover of hookedspur violet was higher in the moderate-severity sites than unburned areas (Table 6).

Old man's whiskers (*Geum triflorum* Pursh) was present only in the central and southern zones. In the central zone, cover of this species did not vary by fire severity. In the southern zone, the highest cover of old man's whiskers was in the unburned areas.

Table 6. Percent canopy cover (means with SE in parentheses, n=3) for indicator species, species of interest and rock as affected by zone and severity interactions at ponderosa pine study sites.

Species	Northern Zone				Central Zone				Southern Zone			
	Burn Severity				Burn Severity				Burn Severity			
	U	L	M	H	U	L	M	H	U	L	M	H
arrowleaf balsamroot (SE)	0.42 ^B (0.24)	8.5 ^A (2.8)	7.7 ^A (3.0)	1.9 ^B (1.9)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)
bastard toadflax (SE)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^B (0)	0 ^B (0)	0 ^B (0)	1.2 ^A (0.63)					
common juniper (SE)	3.6 ^A (1.9)	0 ^B (0)	0 ^B (0)	0 ^B (0)	11 ^A (5.5)	0 ^B (0)	0 ^B (0)	0 ^B (0)	0.03 ^A (0.03)	0 ^A (0)	0 ^A (0)	0 ^A (0)
heartleaf arnica (SE)	0 ^B (0)	0.2 ^A (0.15)	0 ^B (0)	0 ^B (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)
hookedspur violet (SE)	0.08 ^A (0.05)	0.03 ^A (0.03)	0 ^A (0)	0.03 ^A (0.03)	0.03 ^B (0.03)	0.14 ^{AB} (0.14)	0.97 ^A (0.48)	0.42 ^{AB} (0.34)	0 ^A (0)	0 ^A (0)	0.03 ^A (0.03)	0 ^A (0)
northern bedstraw (SE)	2.1 ^A (0.82)	1.4 ^A (0.70)	0.64 ^A (0.20)	1.3 ^A (0.29)	0.89 ^A (0.51)	1.7 ^A (0.18)	1.3 ^A (0.12)	1.3 ^A (0.66)	0.17 ^A (0.10)	0.56 ^A (0.19)	2.0 ^A (0.92)	0.28 ^A (0.24)
old man's whiskers (SE)	0 ^A (0)	0.17 ^A (0.17)	0.06 ^A (0.06)	0 ^A (0)	1.7 ^A (0.85)	0 ^B (0)	0 ^B (0)	0 ^B (0)				
sticky purple geranium (SE)	0 ^B (0)	0.25 ^A (0.21)	0 ^B (0)	0 ^B (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)	0 ^A (0)
western snowberry (SE)	2.9 ^{AB} (1.2)	0.08 ^B (0.08)	1.5 ^{AB} (1.4)	5.4 ^A (1.3)	2.8 ^B (1.6)	7.3 ^{AB} (0.66)	7.8 ^{AB} (0.77)	13 ^A (1.2)	6.0 ^A (1.2)	5.8 ^A (3.1)	5.2 ^A (1.0)	3.1 ^A (1.2)
Woods' rose (SE)	1.2 ^{AB} (0.54)	0 ^B (0)	0 ^B (0)	4.5 ^A (2.0)	0.06 ^A (0.06)	1.1 ^A (0.27)	0.22 ^A (0.22)	0.75 ^A (0.13)	0.69 ^A (0.57)	0 ^A (0)	1.3 ^A (1.2)	0.28 ^A (0.28)
rock (SE)	0.25 ^B (0.25)	0.47 ^B (0.29)	2.5 ^{AB} (0.82)	11 ^A (4.0)	0.39 ^B (0.39)	3.1 ^{AB} (1.4)	0.78 ^{AB} (0.41)	5.7 ^A (0.80)	0.19 ^B (0.10)	4.7 ^{AB} (1.4)	1 ^B (0.67)	8.1 ^A (0.48)

Means in a row with the same letter are not different, Tukey's method, $\alpha = 0.10$. Species and categories included: arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.), bastard toadflax (*Comandra umbellata* (L.) Nutt.), common Juniper (*Juniperus communis* L.), heartleaf arnica (*Arnica cordifolia* Hook.), hookedspur violet (*Viola adunca* Sm.), northern bedstraw (*Galium boreale* L.), old man's whiskers (*Geum triflorum* Pursh), sticky purple geranium (*Geranium viscosissimum* Fisch. & C.A. Mey. ex C.A. Mey.), western snowberry (*Symphoricarpos occidentalis* Hook.), Woods' rose (*Rosa woodsii* Lindl.), and rock. Differing burn severities are abbreviated (U= unburned, L= low, M= moderate, and H= high).

Bastard toadflax (*Comandra umbellata* (L.) Nutt.) only occurred in the southern zone and had the greatest cover in high-severity sites. Northern bedstraw (*Galium boreale* L.) appeared to be insensitive to fire because the cover of this species was similar across all severities in all three zones (Table 6).

Rock cover in high-severity sites was greater than in unburned sites in all zones. In the northern zone, rock cover in the high-severity sites was also greater than in low-severity sites. In the southern zone, rock cover in high-severity sites was greater than moderate-severity sites (Table 6).

When canopy cover was analyzed by functional group, forbs varied by zone ($P = <0.0001$) and severity ($P = <0.0001$), but the interaction was not significant ($P = 0.2209$). The northern zone had the greatest forb cover (Table 7). Canopy cover of forbs in the central and southern zones was similar. Forb cover in moderate- and high-severity sites was similar and greater than forb cover in the unburned areas. Forb cover at low-severity sites was similar to moderate- and high-severity sites as well as unburned areas.

Grass cover varied by zone ($P = <0.0001$) and severity ($P = <0.0001$), but the effects of severity varied by zone ($P = <0.0001$). In the northern zone, grass cover was greatest in the moderate-severity sites, and roughly three times the values present in the other severities (Table 7). In the central zone, grass cover in high-severity sites was greater than in low-severity sites, but similar to unburned and moderate-severity sites. In the southern zone, grass cover in both moderate and high-severity sites was greater than low-severity sites, but similar to unburned sites.

Table 7. Percent canopy cover (means with SE in parentheses, n=3) for functional groups (grasses, forbs and shrubs) and all plants combined (total) as affected by zone, severity and the two factors simultaneously at ponderosa pine study sites on the Black Hills National Forest.

	Forbs Mean (SE)	Grasses Mean (SE)	Shrubs Mean (SE)	Total Mean (SE)
Northern Zone				
Unburned ¹	15 (2.0)	2.4 ^B (0.36)	21 ^A (2.7)	39 ^A (3.6)
Low ¹	25 (2.9)	2.6 ^B (0.40)	16 ^{AB} (1.9)	43 ^A (4.0)
Moderate ¹	26 (2.9)	8.7 ^A (0.85)	11 ^B (2.0)	46 ^A (3.5)
High ¹	20 (2.3)	2.9 ^B (0.39)	21 ^A (2.6)	44 ^A (3.4)
Average ²	22 ^A (2.3)	4.2 (0.35)	17 (1.2)	43 (1.8)
Central Zone				
Unburned ¹	10 (2.3)	2.7 ^{AB} (0.83)	31 ^A (5.5)	43 ^A (5.8)
Low ¹	12 (1.5)	1.7 ^B (0.41)	13 ^B (2.1)	27 ^B (3.1)
Moderate ¹	20 (1.6)	2.7 ^{AB} (0.37)	11 ^B (1.7)	34 ^{AB} (2.7)
High ¹	17 (1.5)	3.6 ^A (0.43)	14 ^B (1.8)	35 ^{AB} (2.0)
Average ²	14 ^B (1.9)	2.7 (0.25)	17 (1.4)	35 (1.7)
Southern Zone				
Unburned ¹	8.5 (1.9)	3.8 ^{AB} (0.40)	7.5 ^A (1.6)	20 ^{AB} (2.6)
Low ¹	8.1 (0.97)	2.7 ^B (0.39)	6.9 ^A (1.5)	18 ^B (1.9)
Moderate ¹	16 (1.9)	4.9 ^A (0.47)	9.6 ^A (1.7)	30 ^A (3.1)
High ¹	15 (1.5)	5.5 ^A (0.55)	3.5 ^A (0.87)	24 ^{AB} (1.8)
Average ²	12 ^B (1.5)	4.2 (0.24)	6.9 (0.74)	23 (1.3)
Average				
Unburned ³	10 ^b (2.4)	3.0 (0.29)	20 (2.0)	34 (2.4)
Low ³	15 ^{ab} (2.8)	2.4 (0.23)	12 (1.1)	29 (2.0)
Moderate ³	21 ^a (2.4)	5.5 (0.42)	11 (1.0)	37 (1.9)
High ³	18 ^a (1.6)	4.0 (0.28)	13 (1.3)	35 (1.6)

Mean separations in a column are included only for main effects or interaction terms where F-tests resulted in P<0.1.

¹Severity by zone interaction means in a column with the same upper case letters are not different, Tukey's method, $\alpha = 0.1$.

²Zone main effect means where the interaction between severity and zone was not significant. Means in a column with the same upper case letters are not different, Tukey's method, $\alpha = 0.1$.

³Severity main effect means where the interaction between severity and zone was not significant. Means in a column with the same lower case letters are not different, Tukey's method, $\alpha = 0.1$.

Shrub cover varied by zone ($P = <0.0001$) and severity ($P = <0.0001$), but again the effects of severity varied by zone ($P = <0.0001$). In the northern zone, shrub cover in high-severity and unburned sites was greater than moderate-severity sites, but similar to low-severity sites (Table 7). In the central zone, the greatest shrub cover occurred in unburned sites while all burned sites had similar shrub cover values. In the southern zone, shrub cover was consistent across all burn severities and the unburned areas.

Total plant cover varied by zone ($P = <0.001$) and by severity ($P = 0.0031$) but the effects of severity varied by zone ($P = 0.0467$) as well. In the northern zone, total cover was consistent across all burn severities and unburned areas (Table 7). In the central zone, total cover was greater in unburned sites than low-severity sites. In the southern zone, moderate-severity sites had greater total cover than low-severity sites.

Frequency of Canada thistle and houndstongue (*Cynoglossum officinale* L.) varied by severity ($P = <0.0001$ and $P = 0.0066$, respectively). No other relationship between invasive species frequency and fire severity were detected based on the extensive invasive species search at ponderosa pine sites. Canada thistle frequency was greatest in the moderate- and high-severity sites, intermediate in low-severity sites and least in unburned sites (Table 8). Zone did not affect Canada thistle frequency ($P = 0.7713$) and the interaction between zone and severity was also unimportant ($P = 0.1439$). Houndstongue frequency was greatest in moderate-severity sites and similar across all other severities (Table 8). Zone did not affect frequency of houndstongue ($P = 0.1049$) and the effect of fire severity was consistent across all zones ($P = 0.6381$).

Table 8. Frequency (% , means with SE in parentheses, $n=3$) of invasive species as affected by fire severity in the ponderosa pine study sites.

Invasive Species	Burn Severity			
	Unburned	Low	Moderate	High

Canada thistle (SE)	3.7 ^C (3.7)	26 ^B (9.2)	70 ^A (3.8)	66 ^A (9.6)
houndstongue (SE)	3.7 ^B (3.7)	7.3 ^B (4.9)	37 ^A (10)	11 ^B (7.8)
Means in a row with the same letter are not different, Tukey's method, $\alpha = 0.10$. Species included: Canada thistle (<i>Cirsium arvense</i> (L.) Scop.) and houndstongue (<i>Cynoglossum officinale</i> L.).				

Although the frequency of some invasive species reached 70%, the canopy cover of individual invasive/exotic species never exceeded 3.5% in the ponderosa pine stands (Figure 3). The highest canopy cover value for an invasive plant was for Canada thistle in the moderate-severity sites (3.4%, ± 0.89).

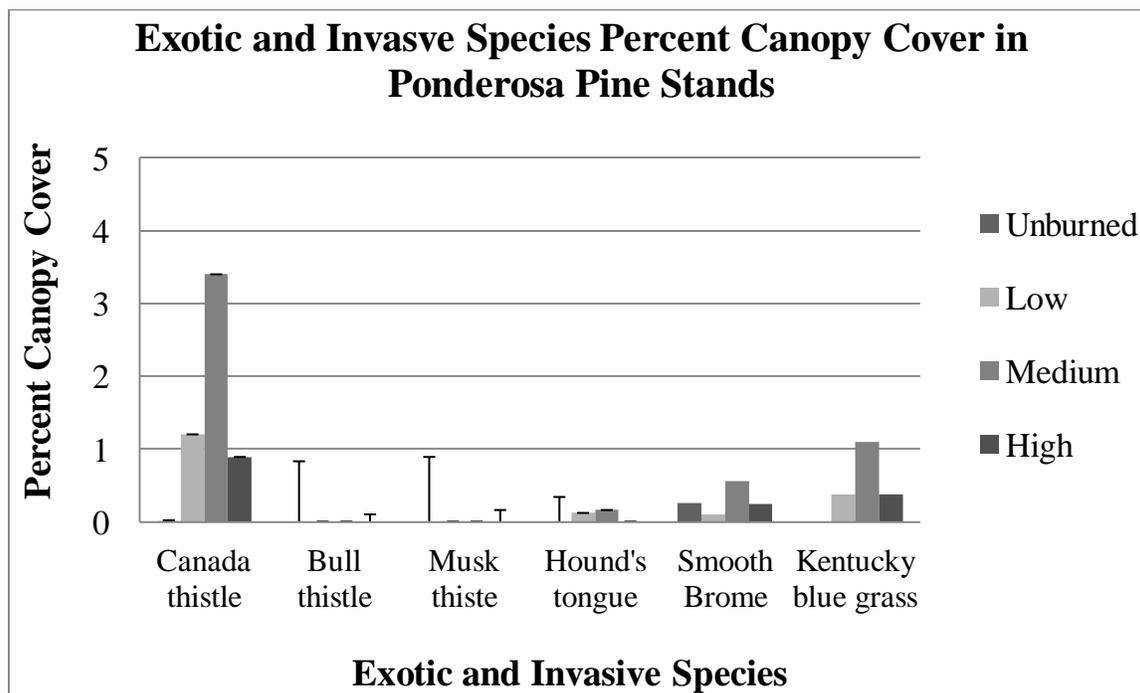


Figure 3. Cover of exotic and invasive species by severity in ponderosa pine sites ten years postfire.

Aspen

Responses of the aspen understory communities to mixed-severity fire differed from ponderosa pine understory communities in that community composition in aspen stands was much more consistent across severities in the northern and central zones. However, results (MRPP) indicated that understory community responses to fire severity did differ between the northern and central zones. The effects of zone and severity can be considered by holding one factor constant while examining different levels of the other (Tables 9 and 10). In the northern zone the unburned community differed from areas that burned at high-severity (Table 9). No other differences were detected in either of the zones (Table 9). Interestingly, communities associated with each of the burn severities were consistent across all severities (Table 10).

Table 9. Comparison of species composition based on canopy cover of understory plants ($\alpha = 0.10$) in Aspen study sites from 2 zones (northern and central) and 3 fire severities (unburned, low and high) using a multi-response permutation procedure (MRPP). The chance corrected within-group homogeneity (A) is presented along with the p-value (P) associated with the A test statistic from the MRPP.

Severity Comparison	Northern Zone		Central Zone	
	A	P	A	P
UNBURNED vs. LOW	-0.028	0.77	0.015	0.32
UNBURNED vs. HIGH	0.055	0.088	0.015	0.34
LOW vs. HIGH	-0.041	0.75	-0.040	0.78

Table 10. Comparison of species composition based on canopy cover of understory plants ($\alpha = 0.10$) grouped by burn severity (unburned, low and high) in Aspen study sites using a multiresponse permutation procedure (MRPP). The chance corrected within-group homogeneity (A) is presented along with the p-value (P) associated with the A test statistic from the MRPP.

	A	P
UNBURNED		
NORTHERN ZONE vs. CENTRAL ZONE	0.017	0.32
LOW-SEVERITY		
NORTHERN ZONE vs. CENTRAL ZONE	0.042	0.22
HIGH-SEVERITY		
NORTHERN ZONE vs. CENTRAL ZONE	-0.040	0.72

The indicator species analysis identified four plant species that likely contributed to community differences detected by the MRPP. These four species were blanket flower (*Gaillardia aristata* Pursh), Gunnison's mariposa lily (*Calochortus gunnisonii* S. Watson), mountain brome (*Bromus marginatus* Nees ex Steud) and slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinnery ssp. *subsecundus* (Link) A. Löve & D. Löve). An additional 23 species of interest, bare ground and litter were analyzed further. Separate analyses of variance were conducted for each of the 4 indicator species along with the other 23 species of interest, bare ground and litter. All plants and sampling categories analyzed using ANOVA are presented in Table 11.

Out of the 29 ANOVA's, 5 species varied by zone or severity. The interaction between zone and severity was not significant in any of the analyses ($0.10 < P < 0.94$) (Table 11). Quaking aspen (*Populus tremuloides* Michx.) was the only species for which cover differed only by zone ($P = 0.0082$) (Table 11). Quaking aspen was most abundant in the northern zone where cover was drastically greater than in the central zone (Table 12). Gunnison's mariposa lily (*Calochortus gunnisonii* S. Watson) was also affected by zone and like quaking aspen its abundance was greater in the northern zone.

Table 11. Results of ANOVA and indicator species analysis conducted on sampling categories and species of interest, in aspen stands, when comparing community composition between severity and zones. ANOVA was used to investigate the effects of fire severity and zone on canopy cover of indicator species, other species of interest, bare ground, litter and rock. Species of interest were selected based on field observations and indicator species had observed indicator values $\geq 50\%$ and p-values ≤ 0.05 in Monte Carlo test of significance using an indicator species analysis.

Species ¹	ANALYSIS OF VARIANCE			INDICATOR SPECIES ANALYSIS	
	Zone Main Effect (P)	Severity Main Effect (P)	Zone x Severity Interaction (P)	Indicator Value	P
Gunnison's mariposa lily	0.069²	0.0031	0.28	69	0.030
quaking aspen	0.0082	0.36	0.69	NA	NA

blanket flower	0.65	0.00040	0.80	50	0.055
purple meadowrue	0.87	0.0035	0.71	NA	NA
slender wheatgrass	0.12	0.0098	0.47	63	0.055
American vetch	0.038	0.42	0.17	NA	NA
blue wildrye	0.54	0.20	0.67	NA	NA
common dandelion	0.24	0.78	0.85	NA	NA
common yarrow	0.37	0.11	0.15	NA	NA
cream pea	0.41	0.87	0.36	NA	NA
flexile milkvetch	0.20	0.90	0.84	NA	NA
fowl bluegrass	0.90	0.98	0.19	NA	NA
Kentucky bluegrass	0.66	0.90	0.56	NA	NA
kinnikinnick	0.46	0.51	0.43	NA	NA
limber honeysuckle	0.52	0.036	0.68	NA	NA
meadow zizia	0.97	0.94	0.90	NA	NA
mountain brome	0.27	0.069	0.40	52	0.051
northern bedstraw	0.68	0.48	0.36	NA	NA
Richardson's needlegrass	0.97	0.65	0.40	NA	NA
rough bluegrass	0.13	0.15	0.42	NA	NA
silvery lupine	0.91	0.24	0.94	NA	NA
slender cinquefoil	0.55	0.042	0.49	NA	NA
sticky purple geranium	0.16	0.31	0.10	NA	NA
Virginia strawberry	0.96	0.22	0.86	NA	NA
western snowberry	0.77	0.21	0.43	NA	NA
white clover	0.32	0.11	0.71	NA	NA
Woods' rose	0.78	0.94	0.86	NA	NA
bare ground	0.35	0.046	0.42	NA	NA
Litter	0.046	0.77	0.79	NA	NA

¹Species of interest and sampling categories included: American vetch (*Vicia Americana* Muhl. ex Willd.), blanket flower (*Gaillardia aristata* Pursh), blue wildrye (*Elymus glaucus* Buckley), common dandelion (*Taraxacum officinale* F.H. Wigg.), common yarrow (*Achillea millefolium* L.), cream pea (*Lathyrus ochroleucus* Hook.), flexile milkvetch (*Astragalus flexuosus* Douglas ex G. Don), fowl bluegrass (*Poa palustris* L.), Gunnison's mariposa lily (*Calochortus gunnisonii* S. Watson), Kentucky bluegrass (*Poa pratensis* L.), kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng), limber honeysuckle (*Lonicera dioica* L. var. *glaucescens* (Rydb.) Butters), meadow zizia (*Zizia aptera* (A. Gray) Fernald), mountain brome (*Bromus marginatus* Nees ex Steud.), northern bedstraw (*Galium boreale* L.), purple meadowrue (*Thalictrum dasycarpum* Fisch. & Avé-Lall.), Table 11 footnote, continued

quaking aspen (*Populus tremuloides* Michx.), Richardson's needlegrass (*Achnatherum richardsonii* (Link) Barkworth), rough bluegrass (*Poa trivialis* L.), silvery lupine (*Lupinus argenteus* Pursh), slender cinquefoil (*Potentilla gracilis* Douglas ex Hook.), slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinners ssp. *subsecundus* (Link) A. Löve & D. Löve), sticky purple geranium (*Geranium viscosissimum* Fisch. & C.A. Mey. ex C.A. Mey.), Virginia strawberry (*Fragaria virginiana* Duchesne), western snowberry (*Symphoricarpos occidentalis* Hook.), white clover (*Trifolium repens* L.), Woods' rose (*Rosa woodsii* Lindl.), bare ground, and litter.

²P-values for significant main effect and interaction terms appear in bold text, while un-bolded P-values indicate that a particular effect or the ANOVA model was insignificant.

Table 12. Percent canopy cover (means with SE in parentheses, n=9) of indicator species and

Species	Zone	
	Northern	Central
Gunnison's mariposa lily (SE)	0.018 ^A (0.0093)	0.0038 ^B (0.0028)
quaking aspen (SE)	15 ^A (3.7)	1.8 ^B (1.3)

Means in a row with the same letter are not different, Tukey's method, $\alpha = 0.10$. Species included: Gunnison's mariposa lily (*Calochortus gunnisonii* S. Watson) and quaking aspen (*Populus tremuloides* Michx.)

The abundance of blanket flower (*Gaillardia aristata* Pursh), Gunnison's mariposa lily, purple meadowrue (*Thalictrum dasycarpum* Fisch. & Avé-Lall.) and slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinnars ssp. *subsecundus* (Link) A. Löve & D. Löve) varied by severity (Table 11). Blanket flower, slender wheatgrass and Gunnison's mariposa lily all appeared to be fire sensitive as the greatest abundance of these species was in unburned sites (Table 13). Purple meadowrue was also more abundant in low-severity sites compared to high-severity sites.

Table 13. Percent canopy cover (means with SE in parentheses, n=6) of indicator species and species of interest in the aspen sites as affected by fire severity.

Species	Burn Severity		
	Unburned	Low	High
blanket flower (SE)	0.22 ^A (0.067)	0 ^B (0)	0 ^B (0)
Gunnison's mariposa lily (SE)	0.028 ^A (0.013)	0.0042 ^B (0.0042)	0 ^B (0)
purple meadowrue (SE)	4.4 ^A (1.5)	3.3 ^A (0.93)	0.35 ^B (0.15)
slender Wheatgrass (SE)	0.23 ^A (0.11)	0.046 ^B (0.046)	0 ^B (0)

Means in a row with the same letter are not different, Tukey's method, $\alpha = 0.10$. Species included: Blanket flower (*Gaillardia aristata* Pursh), Gunnison's mariposa lily (*Calochortus gunnisonii* S. Watson), purple meadowrue (*Thalictrum dasycarpum* Fisch. & Avé-Lall.) and slender Wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinnars ssp. *subsecundus* (Link) A. Löve & D. Löve).

When canopy cover was analyzed by functional group, grass cover was not affected by severity ($P=0.85$), but did vary by zone ($P = 0.079$) and also by the two factors simultaneously ($P = 0.0047$). Grass cover across severities in the northern and central zones was similar except that unburned sites in the central zone had greater grass cover than unburned sites in the northern zone (Table 14).

Forbs varied by severity ($P = <0.0001$) and by the interaction between zone and severity ($P = <0.0001$), but the main effect of zone was not significant ($P=0.43$). In the northern zone, forb cover was greater in the low-severity and unburned sites than the high-severity sites (Table 14). In the central zone, the highest abundance of forbs was in the unburned sites.

Canopy cover of shrubs also varied by severity ($P = 0.0096$) and the interaction between zone and severity ($P = 0.0012$), but the main effect of zone was not significant ($P=0.34$). In the northern zone, shrubs were more abundant in the high-severity sites than the unburned sites (Table 14). In the central zone, shrubs were more abundant in the unburned sites than the low-severity sites.

Total plant cover was affected by severity ($P=0.016$) but the effects of severity varied by zone ($P= <0.0001$). The main effect of zone was not significant ($P=0.21$). In the northern zone, low-severity sites had greater total cover than unburned sites, but not high-severity sites (Table 14). Total plant cover in high-severity and unburned sites in the northern zone was similar. In the central zone, unburned areas had greater total cover than both low and high-severity sites which were similar to one another.

Table 14. Percent canopy cover (means with SE in parentheses, $n=3$) for functional groups affected by zone and severity interactions at aspen study sites.

	Northern Zone	Central Zone
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Functional Group	Burn Severity			Burn Severity		
	U	L	H	U	L	H
Grass (SE)	8.6 ^B (0.56)	15 ^{AB} (2.1)	15 ^{AB} (3.2)	18 ^A (2.0)	13 ^{AB} (1.1)	13 ^{AB} (1.7)
Forb (SE)	38 ^{BC} (2.1)	44 ^B (2.3)	30 ^D (1.6)	51 ^A (1.9)	34 ^{CD} (1.9)	31 ^{CD} (2.4)
Shrub (SE)	11 ^B (2.0)	15 ^{AB} (2.4)	21 ^A (2.8)	23 ^A (2.8)	11 ^B (2.0)	18 ^{AB} (2.6)
Total (SE)	58 ^C (2.9)	73 ^B (4.4)	66 ^{BC} (4.8)	92 ^A (4.5)	58 ^C (3.4)	62 ^{BC} (4.7)

Means in a row with the same letter are not different, Tukey's method, $\alpha = 0.10$. Functional groups included: grasses, forbs and shrubs. Differing burn severities are abbreviated (U= unburned, L= low, M= moderate, and H= high).

The frequency of houndstongue was not affected by severity ($P= 0.4996$), zone ($P= 0.8685$) nor the interaction of these factors ($P= 0.7311$). The frequency of musk thistle also was not affected by severity ($P= 0.3966$), zone ($P= 0.3370$), or the interaction ($P= 0.3966$). The overall F-test for Canada thistle was not significant ($P= 0.2140$). Had we ignored the overall F-test, it would have appeared that Canada thistle frequency was affected by severity. This is most likely caused by the variability between zones that masked the effects of severity. The net result was that the frequency of invasive species did not vary by zone, severity or their interaction. Frequencies of all exotic and invasive species encountered are graphed in Figure 4.

Although the frequency of invasive species reached 61%, canopy cover of individual exotic species, including invasive species, never exceeded 5% in the aspen stands. Invasive species (Canada thistle, bull thistle, musk thistle and houndstongue) never exceeded 1% canopy cover in aspen sites. As in the ponderosa stands, the highest cover was from Canada thistle. This was in the low-severity sites where canopy cover was 1% (± 0.50) (Figure 5).

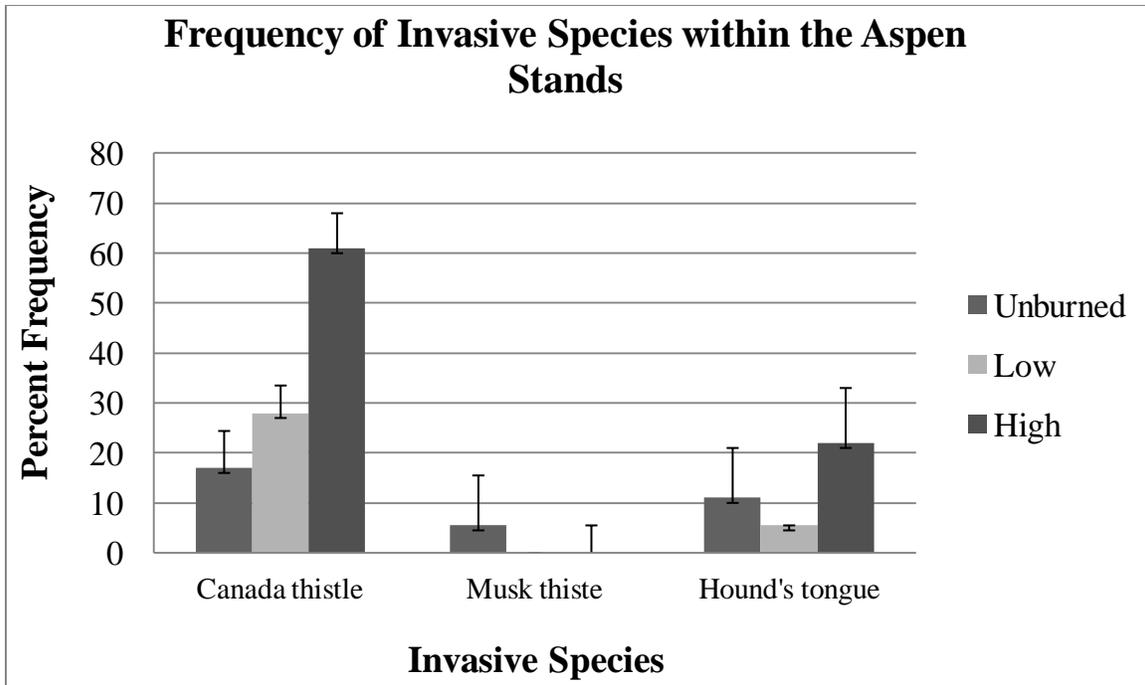


Figure 4. Frequency of invasive species by severity in aspen sites ten years postfire.

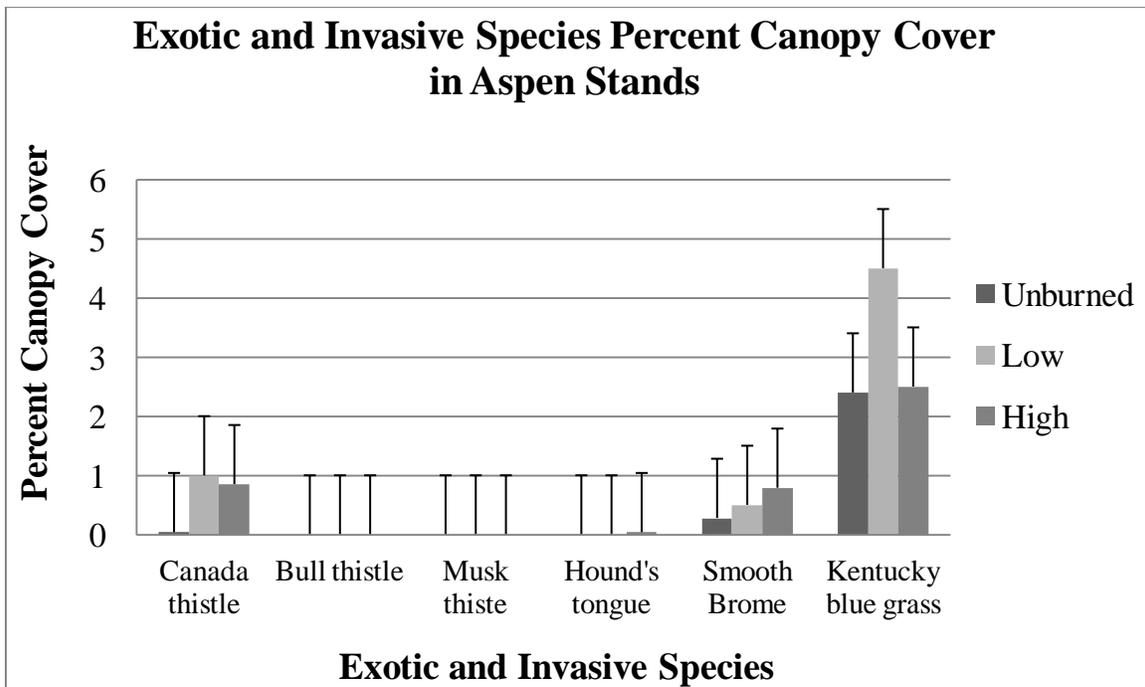


Figure 5. Cover of exotic and invasive species by severity in aspen sites ten years postfire.

DISCUSSION

The Jasper Fire created a very unique landscape in which mosaics of plant communities re-established following the mixed-severity fire. Community dynamics observed over the past 10 years provide insights into both short- and long-term understory responses to mixed-severity fires in ponderosa pine ecosystems. Documenting these changes provides important information to support management decisions in the Black Hills and perhaps elsewhere. As pointed out by Keyser (2007), it is important to explain differences in community composition in-order to understand the rate and amount of recovery that can and will occur following disturbances such as mixed-severity fires.

Differences in understory species composition following the mixed-severity Jasper Fire were more evident in the ponderosa pine study sites than in the aspen study sites. In ponderosa stands, there were many differences in species composition driven by severity and zone simultaneously, while in the aspen stands the only difference detected in understory composition was between the unburned and high-severity sites in the northern zone. Other studies have also documented understory community composition differences resulting from different fire severities. Lentile et al. (2007) examined 8 large fires, 2 each in dry and moist mixed-conifer forests in Montana and 2 in boreal forests in Alaska. During these studies, they concluded that canopy cover and species richness were highly variable among differing burn severities. White et al. (1996) also concluded that fire severity greatly influenced plant community regeneration in conifer forests following a fire in Montana. Armour et al. (1984) also observed differences in canopy cover of various life forms when comparing severities. They found that graminoid canopy cover was lowest in high intensity sites while no significant differences were found in

cover of forbs or shrubs. Ten years after the Jasper Fire, plant communities had diverse results due to the varying landscape and multiple fire severities.

Although the recovery of the understory vegetation initially following the Jasper Fire was quite rapid across the entire area there appear to be substantial differences in total cover when comparing the 10 year to the 5 year data (refer to Figure 3 & Keyser 2007). Even though total cover in the Jasper Fire decreased in the past 5 years, there are studies such as the one conducted by Gildar et al. (2004) and another conducted by Haywood (2011) that concluded fire can increase understory cover. Haywood (2011) concluded that fire, depending on severity, had an overall rejuvenating effect on plant communities in the Kisatchie National Forest, Louisiana. Gildar et al. (2004) concluded that following fire, understory cover returned to past cover levels and in some locations surpassed unburned areas cover in northern Arizona. Our findings are more similar to the work conducted in Arizona than to the study from Louisiana. Although the canopy cover totals appear lower in the 10 year data compared to the 5 year data, total plant cover in ponderosa sites seems to have become dominated by more native perennial plant communities with very few exotics with minor differences observed between severities and zones.

The apparent reduction in total understory plant cover of ponderosa pine sites between 5- and 10-years could have resulted from a number of factors. It is most likely an indication of continued understory plant development. Annuals and biennials likely provided the initial burst of cover immediately following the fire. Then over the years, total cover may have decreased as perennials increased relative to annuals. This becomes apparent when comparing the 2- and 5-year indicator species data (Keyser 2007) with the 10 year data. In the 2- and 5-year data, many annuals and biennials were indicator species while in the 10-year data these species were not

indicators and were not even noted as being present. These species included American dragonhead (*Dracocephalum parviflorum* Nutt.) prickly lettuce (*Lactuca seriola* L.) and littlepod false flax (*Camelina microcarpus* Andr. ex DC.). Orr (1970) reported that American dragonhead exhibited initial prominence following fire in a Ponderosa Pine forest in the Black Hills but greatly declined and even disappeared after the 2nd or 3rd year post-fire. Other studies (Crane et al. 1983 and Brown & DeByle 1989) found similar results suggesting that these species are prominent after disturbances, such as fire, but swiftly decline. Riegel et al. (1995) and sources within support this idea as they have found that early-seral understory species grow rapidly following disturbances, taking advantage of resources. As the canopy closes, years pass and succession occurs, those species are replaced by mid-seral plants that are eventually replaced by late-seral species that can survive in conditions the other two cannot. Laughlin et al. (2004) also documented changes in plant communities that were ultimately attributed to an initial increase in annual and biennial forbs after a fire in ponderosa pine forest in Arizona.

Another factor that could have played a role in the changes in cover observed between year 5 and year 10 after the fire is precipitation. April to September precipitation in 2006, 2007 and 2009 was 51 to 130 mm below the 30 year averages (1971-2000) for April to September (2006-2009 precipitation data came from the Custer RAWS station). This may have influenced growth and development of longer-lived perennial plants that were likely replacing the annual, biennial and short-lived perennials that were more abundant in burned areas the first 5 years following the fire.

Canopy cover data is a reliable measure to describe plant communities (on large and/or small scales) and also allows one to compare species and growth forms (Floyd and Anderson 1982 and sources within). Cover data is a precise measurement as it reduces observer error, and

produces statistically sound data (Daubenmire 1959). Total understory plant cover of the ponderosa pine sites in this study was between the cover classes of 2 (5-25% cover) and 3 (25-50% cover) as described by Bonham et al. (2004). Although total cover is between the categories commonly referred to as low and moderate, plant communities appear to be healthy and diverse with non-native species making up a very small portion of the total cover. These are encouraging results and natural resource managers should expect total native cover will remain stable or perhaps continue to increase in the near future, due to the natural processes of succession. The stable or increasing native plant cover will likely help keep non-native cover relatively low.

The variation of fire severity across the landscape during the Jasper Fire caused changes in functional group composition. As Keyser (2007) pointed out, graminoids are a very important functional group as they offer a great deal of cover to disturbed areas and also provide forage for both wild and domestic herbivores. Ten years after the fire in the ponderosa pine sites, cover of graminoids in the moderate- or high-severity sites was often greater than the unburned or low-severity sites (Table 7). Although high-severity sites supported greater graminoid cover than unburned sites 5 years post-fire (Keyser 2007), by 10-years post-fire, such differences were not detected. The 5-year post-fire results also indicated graminoid cover was greater in low-severity compared to unburned sites (Keyser 2007), but that difference had disappeared by 10 years post-fire (Table 7). Five years post-fire, moderate-severity sites had less graminoid cover than unburned sites (Keyser 2007), but 10 years post-fire, graminoid cover in moderate-severity sites equaled or exceeded that in unburned sites (Table 7). As time passes, graminoid cover seems to be converging across severities and between burned and unburned areas.

Graminoid responses to fire severity appear to be variable. Armour et al. (1984) found that grass cover was lower in areas that burned at high severity while Vose and White (1991) found that following prescribed-fire, some grass species recovered quite rapidly while others did not suggesting that recovery depends upon the species of grass present in an area. The recovery of graminoid species, as well as other understory vegetation, following high-severity burns might also be attributed to reduced competition for below ground resources from overstory species and increased light availability. Naumburg and DeWald (1999), Riegel et al. (1992) and Lieffers and Stadt (1994) all reported different relative abundances of various understory vegetation depending on the density of the overstory. Although the patterns of graminoid abundance relative to fire severity appear to have changed between 5 and 10 years post-fire, abundances of forbs and shrubs appear to have remained fairly constant.

Forb cover may have decreased between 5 and 10 years post-fire, but the general patterns relative to fire severity appear largely unchanged. All burned sites (low, moderate, and high severities) had greater forb cover than unburned areas 5 years post-fire (Keyser 2007). Ten years post-fire, forb cover in moderate- and high-severity sites had greater cover than unburned areas (Table 7). Positive responses of forbs to fire have been documented by others. Laughlin et al. (2004) reported an increase in annual and perennial forbs two years after a fire in Grand Canyon National Park. Similar responses were observed in Oregon where Wroblewski and Kauffman (2003) suggested that fire increased flowering of many forbs, and Pyle and Crawford (1996) found that prescribed fire increased total forb cover and diversity. Forbs appear to be very responsive to reductions in overstory competition (Moore and Deiter 1992) and many fire-tolerant, perennial forbs possess characteristics that allow them to survive and flourish following

fire (Schoennagel et al. 2004). These adaptations and the ability to take advantage of resources following fire make forbs a vital component of post-fire recovery to the Jasper Fire area.

Immediately following the fire, shrubs were scarce life forms across the landscape accounting for very little of the total cover in the burned areas (Keyser 2007). This was mainly due to the loss of the fire-intolerant shrub common juniper (Keyser 2007 and sources within) which disappeared with any type of fire across the burn area. A decrease in shrubs following fire has been documented by others as well. Bartos et al. (1994) documented that 12 years after a prescribed fire near Jackson, WY, shrub production had yet to return to pre-burn production levels. Other studies report different results suggesting that, although shrub abundance generally declines immediately following fire, some species of shrubs will recover to pre-burn conditions relatively quickly. Armour et al. (1984) found that canopy cover of the dominant shrub snowberry (*Symphoricarpos albus* (L.) S.F. Blake), was unaffected by any type of fire treatment while Turner et al. (1997) found that shrub cover was uniformly low in burned areas yet varied by burn severity. By 2010, the shrub component of the understory in the northern and southern zones of the Jasper Fire appear to have recovered to pre-burn abundances (Table 7). The central zone is the only portion of the Jasper Fire where all burned areas support less shrub cover than unburned areas (Table 7). Common juniper was most abundant in the central zone and its disappearance from all burned areas (Table 6) is most likely driving the observed dynamics.

Out of the large number of plant species (~300) encountered in our sampling throughout the Jasper Fire, only a handful were determined to be indicator species 10-years post fire. This suggests that there are fewer differences in understory composition between burned and unburned sites, indicating convergence in understory community composition across the Jasper

Fire. The indicator species analysis identifies plants that are fairly specific to a particular treatment (in our study, the combination of fire severity and zone). The occurrence of indicator species can offer insight about which plants are sensitive to fire and which are not, and in turn help explain observed post fire understory community dynamics.

In the ponderosa pine stands, only one indicator species (old man's whiskers) was identified in unburned areas. Interestingly, 5 years after the fire, seven species, mainly shrubs, were indicators of unburned sites (Keyser 2007). This again suggests that species present only in the unburned areas 5 years ago have been gradually regaining a presence in the burned areas, closing the gap between the understory species composition of the burned and unburned sites. Specifically, some shrubs (western snowberry, Woods' rose, and creeping barberry) have started to come back in the burned sites increasing the similarities in understory composition between the unburned and burned sites. Although it's very easy to focus on the length of time it takes systems to recover following a disturbance it is also important to remember that these systems are very dynamic and may continue to change for very long periods of time without returning to preburn conditions. De Grandprè et al. (1993) present a great example of this as they conducted a study that investigated changes and abundances of understory species on sites that varied in post-fire age from 26 to 230 years in boreal forests in Québec. They concluded that understory recovery and change occurred continuously through time and that succession depended upon life history characteristics. This helps to explain why in some burned areas of the Jasper Fire understory vegetation had returned to postfire conditions while some areas had surpassed preburn conditions and others were still in transition.

As an indicator of unburned areas, old man's whiskers was specific to only areas that burnt under lower fire severities (Table 6). This suggested that it was fire-intolerant, lacked the

ability to recover following moderate- to high-severity fire and is likely adapted to survive in low-light, understory habitats (Keyser 2007), but not sites lacking a forest overstory. According to the USDA Plants Database (2011), old man's whiskers is rhizomatous, has intermediate shade tolerance, and has moderate fire tolerance suggesting that this plant species is capable of living in the low-light understory conditions of ponderosa pine forests. On a broader scale, old man's whiskers response to fire is variable. One study conducted by Bork et al. (1996) found that old man's whiskers increased following prescribed burns in Alberta Canada while Archibold et al. (2003) concluded its recovery varied depending on the season of the burn in Saskatchewan Canada. These differences could obviously be due to varying landscape characteristics as well as differing precipitation amounts and temperatures. Results similar to ours were reported by Walhof (1997) who found that cover and frequency of this plant were significantly less in burned plots compared to unburned plots in southwestern Montana.

Sticky purple geranium and heartleaf arnica were indicators of low-severity sites in the ponderosa stands (Tables 3 and 6). Both species have a higher fire tolerance and are shade tolerant (USDA Plants Database 2011), meaning that they reacted positively to the fire and continued to flourish in areas that left part of the overstory intact. Armour et al. (1984) also found that sticky purple geranium had the highest percent cover in low-severity burns. They concluded that the best explanation for these results, which may apply to certain forbs in our study, was due to the composition present at the time of the fire which is an important factor in the successional changes that occur after fires (Armour et al. 1984). Hookedspur violet was the only indicator of moderate-severity burn sites and bastard toadflax was the sole indicator of high-severity burn sites. Both of these species are rhizomatous which helps protect their below ground structures during fire, allowing them to rejuvenate vegetatively (Larson and Johnson

2007). Due to this trait, the fire possibly favored these plants by stimulating tillering, allowing them to become better established in the higher severity fire areas. Bastard toadflax is also known as a hemiparasite, which means its roots can tap into the roots of other plants stealing water and nutrients (Larson and Johnson 2007). This characteristic provides another mechanism for why this plant acts as an indicator of more severe fires.

In the ponderosa sites, there were several species that expressed interesting results 10 years post-fire in addition to the indicator species. The only plant species for which cover varied solely by zone was creeping barberry. Creeping barberry has high fire tolerance (USDA Plants Database 2011) due to its well-developed rhizomes (Fire Effects Information System 2011) which probably explains why it was not affected by fire severity. Creeping barberry was much more abundant in the northern zone than the central or southern zones suggesting that it does better at higher elevations that receive more moisture. However, it tolerates and grows in a wide range of climates and soils (Fire Effects Information System 2011) and has high drought tolerance (USDA Plants Database 2011), suggesting that it may just be a matter of time before it increases in the central and southern zones.

Flexile milkvetch was more abundant in high-severity burned sites than any other severity. No other studies were found that report responses of this plant to fire. Our results appear to be the first report that flexile milkvetch responds positively to high-intensity fire.

One of the main drivers of the observed decrease in shrub cover was the disappearance of common juniper with any severity of fire. Common juniper was affected simultaneously by zone and severity and was only found in the unburned sites of all three zones. This species is characterized as being highly susceptible to fire (Tirmenstein 1999) and is often described as

lacking fire-surviving regeneration properties (Fire Effects Information System 2011). Due to these properties and its slow growth rate (USDA Plants Database 2011), it will likely take a long time for common juniper abundance to return to pre-burn levels. Alternatively, it may remain a minor component of the understory communities of the Jasper Fire area.

Arrowleaf balsamroot was only encountered in the northern zone, with greater cover in low- and moderate-severity sites compared to the unburned and high-severity sites. Therefore, it seems that this plant grows in higher elevation areas of the Black Hills and responds positively to low fire severity. However, according to the USDA Plants Database (2011), this plant has a high fire tolerance. Wright et al. (1979) point out that arrowleaf balsamroot spreads by sprouts from a caudex increasing its fire tolerance and improving its ability to return following low- and moderate fire. Regeneration from seed may be more important following high-severity fire because mature plants will likely be damaged or killed. Recovery from seed is expected to take longer, and would help explain the lower abundance of arrowleaf balsamroot in high-severity fire sites. Merrill et al. (1980) found that arrowleaf balsamroot production was consistently higher on burned than unburned areas following a prescribed fire in a ponderosa pine forest and adjacent montane grassland in Idaho that was most likely similar to our low- and moderate-severity sites. However, differences observed by Merrill et al. (1980) were never great enough to be significant. We found that arrowleaf balsamroot abundance was not consistently higher in burned areas, specifically not in high-severity sites. The increased abundance we documented in low- and moderate-severity sites is consistent with the results reported by Merrill et al. (1980) because the prescribed fire they studied was likely low- to moderate-severity.

Northern bedstraw exhibited a zone by severity interaction, but there were no significant differences found between severities within any of the zones. This suggests that this plant is

insensitive to fire, but it is characterized as having low fire tolerance (USDA Plants Database 2011), suggesting that what we observed is an uncommon response to fire. Bartos et al. (1994) also point to this, as they documented that forbs including northern bedstraw, had not returned to pre-burn levels 12 years after a prescribed fire in northwestern Wyoming. These results point to the fact that not all species that are fire sensitive were greatly harmed by the fire, giving hope that plant communities throughout the burn area will return to pre-fire conditions over time.

In the Black Hills, aspen stands account for only 4% of the forested landscape (Keyser et al. 2005) and although this is a small portion of the total area, aspen is a vital component of this ecosystem. On this landscape, small aspen clones are interspersed throughout the massive ponderosa pine forests and support a multitude of plant species not present elsewhere in this ponderosa pine dominated landscape. Studies like the one conducted by Kuhn et al. (2011) along the Sierra Nevada and Cascade Range of northeastern California highlight the major contributions aspen stands make to plant species diversity and richness in conifer dominated ecosystems. Aspen stands of the Black Hills provide food and cover for wildlife and domestic animals and support a vast array of plant species providing pockets of diversity to this otherwise homogenous ecosystem (Keyser et al. 2005).

The understory vegetation in the aspen stands appeared to lack many of the community differences that were observed in the ponderosa pine sites from different zones or fire severities. This is likely attributed to aspen stands being disturbance-dependent and adapted to fire (Bartos 2001) so it makes sense that the understory vegetation would also be adapted to fire. Fire stimulates aspen regeneration and removes conifers which helps reduce their encroachment into aspen stands (Jones and DeByle 1985). Keyser et al. (2005) found that the amount of ponderosa pine regeneration in aspen clones was substantially reduced where fire, specifically high-severity

fire, had occurred. The plant species within these aspen groves appear to have become somewhat adapted to fire, thus increasing their tolerance as well as lessening effects on regeneration and growth. Studies suggest that ecosystems historically characterized as fire-maintained systems have understory plants that continue to display resiliency to fire (Metlen and Fiedler 2006, Antos et al. 1983, Metlen et al. 2004). Due to these adaptations in the understory, it appears that there are very few differences that occurred in the aspen stands. These sites appear to have regenerated quicker than the ponderosa pine sites and are dominated by native perennial plant communities which have, in many cases, surpassed pre-fire conditions.

Functional group composition in the aspen sites was more consistent across severities than observed in the ponderosa pine sites. In the aspen sites graminoid cover was unaffected by fire severity as unburned, low and high fire severities showed no differences in canopy cover (Table 14). This is very different from what others have found. Bartos et al. (1994) reported that graminoid production was reduced by burning and differed across severities, specifically high-severity burns were much less favorable for graminoid growth than moderate- or low-severity burns in aspen stands of northwestern Wyoming. Dodson et al. (2008) reported a loss of 6.1% graminoid cover on burned sites compared to unburned sites in a coniferous forest in central Washington State and Turner et al. (1997) found that graminoid cover was significantly greater in lighter burned areas than more intensely burned areas at three locations in the Yellowstone Fire. These findings suggest that graminoid cover and production, in the Black Hill study areas, was impacted less by fire compared to other areas. This also demonstrates that aspen stands are displaying very few differences between burned and unburned sites 10 years postfire compared to ponderosa pine sites.

Forbs dominated the understory composition in the aspen stands, but they responded to severity in a much different manner than in the ponderosa sites. In aspen sites, forb cover decreased with both high- and low-severity fire in the central zone, while cover of forbs in the northern zone only decreased with high-severity fire (Table 14). This is different than what other studies have found. For example, a similar study by Bartos et al. (1994) found that forbs increased immediately following fire, regardless of severity. Two years after the fire, forb production peaked and all 3 fire severities (low, moderate, and high) were significantly higher than the controls (Bartos et al. 1994). Forb production fluctuated for 10 years after which high- and moderate-severities were significantly higher than control areas (Bartos et al. 1994). Results presented in this thesis were quite different from those of Bartos et al. (1994), possibly because some forb species in their study were aggressive “pioneer” species which dominated the understory after the fire, limiting resources and opportunities for other species to recover. The differences between zones could once again be attributed to variation between the northern and central zones. Such differences include higher elevations, and cooler, wetter conditions existing in the northern zone.

In the central zone, shrub cover in the aspen sites that burned at low severity was reduced to half the value measured in unburned sites, while in the northern zone, shrub cover in unburned sites was approximately half the value measured in sites that burned at high severity (Table 14). Competition for resources from the forest overstory that was removed was likely reduced, especially in areas that burned at high severity. The fact that shrub species vary greatly in their response to fire (Riegel et al. 1992) and the many different re-growth (soils, moisture) opportunities available in the different zones, likely drove the dynamics we observed here. Unlike our results, Bartos et al. (1994) found that shrubs in a similar study were harmed by most

fire severities and never returned to preburn conditions. Griffis et al. (2001) also found that native shrub species decreased significantly in response to wildfire in ponderosa pine forests of northern Arizona. Bartos et al. (1994) also points out that numerous factors such as preburn condition, fire damage, use by ungulates, and postfire competition can all affect shrub recovery leading to different results in the years following a fire. Although the above studies looked at many different shrubs, some similar to our study and some not, our overall results of shrub response to fire differed from them. This could possibly suggest that shrub response to fire is hard to predict and variable from location to location, mainly due to different shrubs responding differently to fire. The results of our study are also important for managers interested in increasing shrub cover in the central portion of the Black Hills and similar areas. Because of this, high-severity fire could possibly be utilized as a management tool to use in these areas, focusing on species that would respond positively to fire. On a landscape scale, the increase in shrub cover in these habitats might counter the loss of shrubs in other zones and forest types. Overall, shrub cover in burned areas appears to have either surpassed unburned conditions (northern zone) or is at least close to being the same as unburned conditions (central zone). This provides further evidence that overall recovery in the aspen stands appears more rapid than the ponderosa sites, which is probably due to aspen systems being disturbance dependent (Bartos 2001) and thus the understory species are also somewhat fire-tolerant, taking less time to regenerate.

Similar to the discussions above regarding total plant cover and functional groups, species-level understory responses to fire in aspen sites were less variable than ponderosa pine sites. Indicator species were only detected in unburned areas and there were only three: Gunnison's mariposa lily, blanket flower, and slender wheatgrass. Blanket flower has low fire

tolerance (USDA Plant Database 2011), suggesting that this plant is probably specific to only unburned areas which is consistent with our results. Gunnison's mariposa lily has moderate fire tolerance and slender wheatgrass has high fire tolerance (USDA Plant Database 2011). The fact that all three of these species had very low cover values (less than 1% even in the unburned areas) suggests that they were flagged as indicator species solely because they were consistently present, although scarce in the unburned areas and generally absent from the other areas. The scarcity of these species across the Jasper Fire is possibly due to them being minor components of the current plant communities throughout the entire landscape caused by competition from other species. The very small number of indicator species suggests that there are few differences between the burned and unburned sites in the aspen stands.

Some differences in understory community composition are still evident between areas that burned at different severities and none of the same indicator species were identified 5 and 10 years postfire in both the ponderosa and aspen sites. It appears Keyser's (2007) conclusion that understory species composition was still changing 5 years after is applicable 10 years postfire. That being said, we identified several lines of evidence suggesting understory communities are becoming more similar to one another and to unburned areas in both ponderosa and aspen sites. Our findings and those of Keyser (2007) emphasize the importance of long-term monitoring following disturbances as large and variable as the Jasper Fire.

It is also interesting to consider that between the indicator species analyses and the ANOVA conducted, only 5 species displayed differences in abundance across severities and zones in the aspen sites while 15 displayed such differences in the ponderosa pine sites. This provides further evidence, suggesting that there are fewer differences in composition between burned and unburned areas in the aspen sites compared to the ponderosa sites.

Woods' rose was affected by zone and severity in the ponderosa pine sites, but was not affected by either in the aspen sites. This result can be explained by the consistent abundance of Woods' rose across the aspen sites compared to inconsistent presence and low abundances in the ponderosa sites. The same can be said of flexile milkvetch, western snowberry and northern bedstraw as their abundances changed with zone and severity in the ponderosa sites, but not in the aspen sites. These differences observed in the patterns of occurrence between the ponderosa pine sites and aspen sites could be due to different growing conditions, prior seed banks, or competition from other more dominant species which could lead to less consistency across the ponderosa sites.

Aspen (aspen sapling regeneration ≤ 1 m) was the only species that was solely affected by zone in the aspen sites. It was much more abundant in the northern zone compared to the central zone. This suggests that aspen abundance in the Jasper Fire was associated with an elevation gradient as well as differing site conditions. Kulakowski et al. (2006) also reported that aspen dynamics, in the Flat Top area of Colorado, were associated with an elevation gradient. They found that throughout their study area, aspen stands increased with increasing elevation up to 3000 m. Although this is not an exact match to what we found, it does support that aspen communities respond to differences in elevation, suggesting why there was such a difference in our study between the two zones. Kulakowski et al. (2006) also concluded that direct competition from conifers could also affect the development of aspens. This is most often caused by natural forest cycles, because aspen is usually not capable of maintaining long-term dominance without stand replacing disturbance, thus is overtaken by conifers. This might have also contributed to the differences we observed between the two zones. The northern zone had a

bigger concentrated area burn at high severity, allowing for more aspens to develop after the fire compared to the central zone (Figure 1).

Another interesting result was that the zone main effect of American vetch was significant, but the overall model was not. American vetch has a moderate fire tolerance and typically increases after fire (Fire Effects Information System 2011). This explains its consistent presence across our study plots. A study by Cooper et al. (2007) found that cover of forbs, such as American vetch, did not differ between burned and unburned macro-plots. Another study by Amour et al. (1984) found that forbs, including American vetch, were more common on low-severity sites, but that overall forb cover remained fairly uniform across fire intensities and found few significant changes through time. These findings are consistent with our results.

Purple meadowrue varied by severity in the aspen sites. Its abundance was greatest in the unburned and low-severity sites compared to high-severity sites suggesting that it is fire sensitive. Although not much has been published about the fire effects on purple meadowrue specifically, a similar species, early meadowrue (*Thalictrum dioicum* L.), is most likely to survive cool fires that don't consume duff, but not severe, hot fires (Fire Effects Information System 2011). This supports our findings, as purple meadowrue's abundance was obviously affected by high severity fire to a much greater degree than it was affected by the cooler, low fire severity.

Changes in environmental conditions brought about by the Jasper Fire allowed exotic species to establish (Keyser 2007). Although many areas still support exotic species 10 years after the fire, their abundance throughout the area affected by the Jasper Fire seems to have remained fairly constant over the past 5 years. Ten years after the fire, no individual exotic

species had a canopy cover value exceeding 5% in either the ponderosa pine or aspen sites.

These results supported our hypothesis that no exotic plant would have a canopy cover value exceeding 10% in either the ponderosa pine or aspen sites. As observed 5 years after the Jasper Fire (Keyser 2007), most of the exotic species encountered were not invasive. Rather, most are considered naturalized to the area, including Kentucky bluegrass and dandelion (Keyser 2007).

These results suggest that invasive species, although present make up a minute portion of the total cover in the Jasper Fire area. Other studies have found quite opposite results, reporting invasive species becoming much bigger threats following fire than what we observed. Crawford et al. (2001) found that after several widespread fires in northern Arizona, cover of exotic species was 26%. Griffis et al. (2001) also reported increases in the abundance of non-native species and found a considerable increase in non-native forbs in areas that had been thinned in addition to having prescribed fire treatments applied following stand-replacing fires in northern Arizona.

Very few of the exotic plants encountered in our study were considered invasive. Kentucky bluegrass had the highest cover value of non-natives in aspen sites (4.5% in low severity) and the second highest cover value in the ponderosa sites (1.1% in moderate severity). Kentucky bluegrass is not considered a threat in the Black Hills and no urgent management attention is needed at this time. Canada thistle is a species of concern in the Black Hills and is invasive. Five years postfire, Canada thistle was the only invasive species of concern, having canopy cover values of 2-4% in the moderate and high severity burn sites (Keyser 2007). Ten years after the fire, Canada thistle remains a concern, but did not appear to increase in abundance. Although it had the greatest cover of all invasive species encountered, the values (3.4% in moderate severity ponderosa sites and 1% in low severity aspen sites) were still very low. Houndstongue is also an invasive and a species of concern, but its abundance (0.16% in

high severity in ponderosa sites and .04% in high severity aspen sites) was minute compared to Canada thistle and also not considered a detrimental threat.

Fire severity has been reported by others to have very noticeable affects on cover and overall presence of exotic plants following fire. Turner et al. (1997) reported cover of opportunistic plants such as Canada thistle increased with fire severity and Crawford et al. (2001) also found that exotic plant cover increased with severity, specifically with high-severity fires. Griffis et al. (2001) also reported that high-severity fires facilitated exotic species establishment in their study. Due to the intensity of the Jasper Fire and findings of others, the response of exotic and invasive species was of great concern for future management of this area. However, this concern has yet to be realized as cover values of Canada thistle, the species which had the highest invasive cover value, did not vary greatly by severity 10 years after the fire (<1 – 3.4% in ponderosa sites and <1- 1% in aspen sites).

Interestingly, the frequency data of the exotic and invasive species in our study may have different implications. In the ponderosa sites, only three species were reported but percent frequency of these exotics ranged from 3.7-70% (Figure 4). Similarly in the aspen sites, only three species were once again documented and percent frequency ranged from 5.5-61% (Figure 7). In both the ponderosa and aspen sites, the highest percent frequency was from Canada thistle. Fire severity once again affected where invasive species were more prevalent as high- and moderate-severities hosted more Canada thistle than low-severity or unburned sites in the ponderosa. In the aspen sites, high-severity sites also had significantly higher frequencies than low or unburned sites. Houndstongue is also very widespread across all of the burned sites in both ponderosa and aspen sites. These data suggest that the low cover values of exotic species in the Jasper Fire could provide a false sense of security because they are present throughout the

landscape and poised to increase following future disturbances, such as future prescribed or wild fire occurrence.

Although Canada thistle is present in the burn area, its cover is not excessive. This supports what Travnicek et al. (2005) found which suggested that although Canada thistle densities increase after fire, the increase may be quite brief. The presence of the other exotic species is also not of great concern presently as their cover values are also very small. Managers should be optimistic about existing efforts to manage exotic and invasive plants because these species have low individual cover values and there have been no significant increases over the past 5 years. To our knowledge, herbicide treatment of weeds in our study area was only conducted in the central zone, by spot spraying a few occurrences of leafy spurge (*Euphorbia esula* L.). This spraying was coordinated with the Black Hills Forest Service and the Rocky Mountain Research Station to ensure that minimal effects would be seen in the study plots. The results from the invasive species analysis suggest that these unwanted plants will not become a problem in the near future, in part because of successful invasive plant management efforts being implemented throughout the Black Hills and the apparent natural resistance of the studied ecosystem to these species. Monitoring of these species should continue to further ensure that invasive species do not become a problem throughout the Jasper Fire area.

CONCLUSIONS & MANAGEMENT IMPLICATIONS

The Jasper Fire and its immediate and long-term influences on understory communities have provided tremendous opportunities to observe the effects of a large mixed-severity fire in a ponderosa pine forest interspersed with aspen stands. With the many challenges and restrictions managers and policy makers are experiencing in respect to managerial response to fire (Provencher et al. 2007; Moore 2004; Jackson & Moore 1998), this study has provided valuable insights that are otherwise fairly rare and limited on today's landscapes. The conclusions drawn from this study will assist in the development of post-fire management tactics and provide information about postfire understory composition and indications of trajectories of future understory community change following a large mixed-severity wildfire.

Prior to the Jasper Fire, the understory was characterized as a shrub dominated system (Keyser 2007) with sparse amounts of graminoids and forbs strewn within. Ten years after the fire, it appears that the understory vegetation has continued to change significantly, even in the most recent 5 years. In the ponderosa pine sites five years after the fire, areas burned at moderate- and high-severity levels had an understory dominated by forbs and graminoids, while the areas burned at low-severity sites remained relatively similar to unburned sites. The 10-year results were slightly different. Forbs still dominate the understory composition but shrubs now comprise more of the overall composition than graminoids. Results also indicated that differences between functional group cover across the different severities, although still evident, are becoming less pronounced. The 10-year analyses identified very few indicator species in the ponderosa sites compared to five years ago (9 in 2010 and 37 in 2005). Although understory composition was not determined in aspen stands during the 5 year evaluation, these sites had

even fewer indicator species (4) than the ponderosa pine sites 10 years postfire. These results indicate, that convergence is occurring in understory composition between burned (low, moderate and high burn severities) and unburned sites in ponderosa, and especially in the aspen ecosystems. We have also concluded that ten years post fire, the understory vegetation appears to have become dominated by native perennial plant communities with very few exotic and invasive species present. Although many managers are concerned about returning these communities to conditions similar to those prior to the Jasper Fire, we have concluded that the present plant communities given time, could possibly have improved diversity and vigor than pre-burn conditions exhibited.

Aspen sites, although a small portion of the landscape, provide pockets of diversity in a rather homogenous landscape (Keyser et al. 2005), making their presence a vital component of areas supporting evergreen forests. As previously stated, very few differences existed 10 years after the Jasper Fire between the burned and unburned sites within the aspen communities. This suggests that the aspen sites and the associated understory communities are adapted to fire and disturbance-dependent (Bartos et al. 2001; Jones and Debyle 1985), ultimately leading to a quicker recovery to pre-burn composition than burned areas in the ponderosa sites. The diverse seed sources from the aspen sites could be very beneficial and important in the overall recovery of the Jasper Fire areas. Due to possible adaption to fire, these small pockets of diversity could potentially increase opportunities for re-growth following a disturbance as variable as the Jasper Fire by providing substantial viable seed banks (Ferrandis et al. 1996) that might otherwise not be available. Minor differences in functional group cover across fire severities 10 years after support the conclusion that aspen understory communities are fire-adapted. Prescribed fire should be considered to help maintain aspen across the landscape with a diverse mix of

understory communities and reduce the chance of conifer encroachment (Bartos et al. 1994). A diverse mix of aspen understory communities will maintain a source of propagules to support understory community development following future fires.

Invasive and exotic species presence is related to fire severity, as cover and frequency both appear to be greater in moderate- and high-severity burn areas. As mentioned earlier, it should be comforting to managers that these species are a minor part of the understory communities and that recent management efforts for invasive species have been successful. Invasive species management including monitoring must continue to ensure that these plants do not become a concern. It is widely accepted that noxious and invasive plants strive for opportunities to get established and increase in abundance following disturbances (Crawford et al. 2001), so this threat should be considered, especially if prescribed fire is used to reduce standing dead and litter resulting from the Jasper Fire.

Overall, we concluded that understory plant communities across the Jasper Fire are dominated by native perennial plant communities with exotic and invasive species not being a current threat. The variability in regeneration we documented across the Jasper Fire supports the conclusion reached by Keyser et al. (2008) that post-fire rehabilitation efforts, if implemented, need to be designed on a site-specific basis. The differences also indicate that the diversity of these native perennial plant communities can be managed to satisfy an equally diverse mix of management objectives. Using an adaptive management approach and focusing management efforts on individual site and burn severity responses will not only increase the likelihood of recovery, but will also benefit both understory and overstory vegetative health in the Jasper Fire area.

Long-term research is rare, especially concerning understory response to fire in ponderosa pine ecosystems (Crawford et al. 2001). The variability associated with understory and overstory composition following mixed-severity fires documented in this thesis and by Keyser et al. (2008) emphasizes the importance of continued long-term research and monitoring. Future research will improve our understanding of ecosystem responses, recovery pathways and assist managers when selecting the mix of management practices most likely to achieve postfire vegetation objectives. Postfire community dynamics involve ongoing processes and living ecosystems, so only time will tell what the actual recovery and composition will be following a very variable mixed-severity fire. Only continued long-term monitoring and research will be able to fully capture the complex transformations and community development.

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APPENDICES

Appendix 1

Table A1.1. Analysis of arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	37	3.3	11	<.0001
Error	24	7.1	0.30		
Total	35	44			
Zone Main Effect	2	23	12	40	<.0001
Treatment Main Effect	6	4.5	1.5	5.1	0.0074
Zone by Treatment Interaction	3	9.0	1.5	5.1	0.0017

Table A1.2. Analysis of bastard toadflax (*Comandra umbellata* (L.) Nutt) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	2.1	0.19	3.8	0.0029
Error	24	1.2	0.050		
Total	35	3.3			
Zone Main Effect	2	0.38	0.19	3.8	0.036
Treatment Main Effect	6	0.57	0.19	3.8	0.023
Zone by Treatment Interaction	3	1.2	0.19	3.8	0.0080

Table A1.3. Analysis of Canada thistle (*Cirsium arvense* (L.) Scop.) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	17	1.5	3.2	0.0087
Error	24	11	0.48		
Total	35	28			
Zone Main Effect	2	2.1	1.1	2.2	0.13
Treatment Main Effect	6	12	4.1	8.7	0.0005
Zone by Treatment Interaction	3	2.1	0.36	0.75	0.62

Table A1.4. Analysis of common juniper (*Juniperus communis* L.) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	24	2.2	3.6	0.0042
Error	24	15	0.61		
Total	35	39			
Zone Main Effect	2	2.5	1.3	2.1	0.15
Treatment Main Effect	6	14	4.7	7.7	0.0009
Zone by Treatment Interaction	3	7.6	1.3	2.1	0.094

Table A1.5. Analysis of creeping barberry (*Mahonia repens* (Lindl.) G. Don) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	54	4.9	9.0	<0.0001
Error	24	13	0.54		
Total	35	67			
Zone Main Effect	2	49	25	45	<0.0001
Treatment Main Effect	6	2.2	0.73	1.3	0.29
Zone by Treatment Interaction	3	2.5	0.41	0.76	0.61

Table A1.6. Analysis of flexile milkvetch (*Astragalus flexuosus* Douglas ex G. Don) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	16	1.5	3.9	0.0026
Error	24	9.1	0.38		
Total	35	25			
Zone Main Effect	2	2.1	1.0	2.8	0.084
Treatment Main Effect	6	11	3.7	9.9	0.0002
Zone by Treatment Interaction	3	2.9	0.47	1.3	0.32

Table A1.7. Analysis of hairystem gooseberry (*Ribes hirtellum* Michx.) percent canopy cover in various treatment and zone combinations in the Ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	0.23	0.021	1.0	0.47
Error	24	0.50	0.021		
Total	35	0.73			
Zone Main Effect	2	0.042	0.021	1.0	0.38
Treatment Main Effect	6	0.063	0.021	1.0	0.41
Zone by Treatment Interaction	3	0.13	0.021	1.0	0.45

Table A1.8. Analysis of heartleaf arnica (*Arnica cordifolia* Hook.) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	0.30	0.028	2.6	0.023
Error	24	0.25	0.011		
Total	35	0.56			
Zone Main Effect	2	0.055	0.028	2.6	0.093
Treatment Main Effect	6	0.083	0.028	2.6	0.074
Zone by Treatment Interaction	3	0.17	0.028	2.6	0.042

Table A1.9. Analysis of hookedspur violet (*Viola adunca* Sm.) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	2.2	0.20	2.9	0.014
Error	24	1.7	0.069		
Total	35	3.9			
Zone Main Effect	2	1.0	0.51	7.3	0.0033
Treatment Main Effect	6	0.28	0.095	1.4	0.28
Zone by Treatment Interaction	3	0.91	0.15	2.2	0.081

Table A1.10. Analysis of northern bedstraw (*Galium boreale* L.) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	4.0	0.37	2.0	0.083
Error	24	4.5	0.19		
Total	35	8.5			
Zone Main Effect	2	1.1	0.56	3.0	0.072
Treatment Main Effect	6	0.45	0.15	0.80	0.51
Zone by Treatment Interaction	3	2.5	0.41	2.2	0.080

Table A1.11. Analysis of old man's whiskers (*Geum triflorum* Pursh) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	3.1	0.28	3.2	0.0090
Error	24	2.1	0.089		
Total	35	5.2			

Zone Main Effect	2	0.44	0.22	2.4	0.11
Treatment Main Effect	6	0.69	0.23	2.6	0.078
Zone by Treatment Interaction	3	2.0	0.33	3.7	0.0098

Table A1.12. Analysis of rock clematis (*Clematis tenuiloba* (Nutt.) Torr. & A. Gray var. *tenuiloba* (A. Gray) J. Pringle) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	2.2	0.20	1.5	0.21
Error	24	3.2	0.13		
Total	35	5.4			
Zone Main Effect	2	0.22	0.11	0.82	0.45
Treatment Main Effect	6	0.44	0.15	1.1	0.37
Zone by Treatment Interaction	3	1.5	0.25	1.9	0.12

Table A1.13. Analysis of roughleaf ricegrass (*Oryzopsis asperifolia* Michx.) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	0.078	0.0071	1.00	0.47
Error	24	0.17	0.0071		
Total	35	0.25			
Zone Main Effect	2	0.014	0.0071	1.0	0.38
Treatment Main Effect	6	0.021	0.0071	1.0	0.41
Zone by Treatment Interaction	3	0.043	0.0071	1.0	0.45

Table A1.14. Analysis of sticky purple geranium (*Geranium viscosissimum* Fisch. & C.A. Mey. ex C.A. Mey) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	0.37	0.034	2.4	0.037
Error	24	0.34	0.014		
Total	35	0.72			
Zone Main Effect	2	0.068	0.034	2.4	0.12
Treatment Main Effect	6	0.10	0.034	2.4	0.095
Zone by Treatment Interaction	3	0.20	0.034	2.4	0.061

Table A1.15. Analysis of strict blue-eyed grass (*Sisyrinchium montanum* Greene) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	0.41	0.037	1.6	0.18
Error	24	0.58	0.024		
Total	35	0.99			
Zone Main Effect	2	0.075	0.037	1.6	0.23
Treatment Main Effect	6	0.11	0.037	1.6	0.23
Zone by Treatment Interaction	3	0.22	0.037	1.6	0.21

Table A1.16. Analysis of western snowberry (*Symphoricarpos occidentalis* Hook.) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	28	2.5	5.0	0.0005
Error	24	12	0.51		
Total	35	40			
Zone Main Effect	2	12	5.8	11	0.0003
Treatment Main Effect	6	3.5	1.2	2.3	0.10
Zone by Treatment Interaction	3	13	2.1	4.1	0.0055

Table A1.17. Analysis of Woods' rose (*Rosa woodsii* Lindl.) percent canopy cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	11	1.0	3.5	0.0047
Error	24	6.9	0.29		
Total	35	18			
Zone Main Effect	2	0.57	0.29	1.0	0.38
Treatment Main Effect	6	2.9	0.95	3.3	0.037
Zone by Treatment Interaction	3	7.8	1.3	4.5	0.0035

Table A1.18. Analysis of percent bare ground cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	73	6.6	5.7	0.0002
Error	24	28	1.2		
Total	35	101			
Zone Main Effect	2	1.8	0.92	0.79	0.47
Treatment Main Effect	6	65	22	19	<0.0001
Zone by Treatment Interaction	3	6.2	1.0	0.89	0.52

Table A1.19. Analysis of percent litter cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	32	2.9	1.0	0.46
Error	24	69	2.9		
Total	35	101			
Zone Main Effect	2	6.5	3.3	1.1	0.34
Treatment Main Effect	6	11	3.5	1.2	0.32
Zone by Treatment Interaction	3	15	2.5	0.88	0.53

Table A1.20. Analysis of percent rock cover in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	34	3.1	7.9	<0.0001
Error	24	9.4	0.39		
Total	35	44			
Zone Main Effect	2	0.52	0.26	0.66	0.52
Treatment Main Effect	6	28	9.5	24	<0.0001
Zone by Treatment Interaction	3	5.3	0.88	2.2	0.074

Appendix 2

Table A2.1. Analysis of present canopy cover of grasses in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F value	P
Model	11	105	9.6	3.6	0.0042
Error	24	64	2.7		
Total		169			
Zone Main Effect	2	29	14	5.4	0.011
Treatment Main Effect	3	45	15	5.7	0.0043
Zone by Treatment Interaction	6	31	5.1	1.9	0.12

Table A2.2. Analysis of present canopy cover of forbs in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	323	29	3.3	0.0067
Error	24	212	8.8		
Total		535			
Zone Main Effect	2	126	63	7.1	0.0038
Treatment Main Effect	3	154	54	5.8	0.0040
Zone by Treatment Interaction	6	44	7.4	0.84	0.55

Table A2.3. Analysis of present canopy cover of shrubs in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	258	24	1.1	0.41
Error	24	517	22		
Total		775			
Zone Main Effect	2	182	91	4.2	0.027
Treatment Main Effect	3	14	4.8	0.22	0.88
Zone by Treatment Interaction	6	62	10	0.48	0.82

Appendix 3

Table A3.1. Analysis of presence or absence of bull thistle (*Cirsium vulgare* (Savi) Ten.) in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	10	0.92	1.0	0.47
Error	24	22	0.92		
Total	35	32			
Zone Main Effect	2	1.83	0.92	1.0	0.38
Treatment Main Effect	3	2.8	0.92	1.0	0.41
Zone by Treatment Interaction	6	5.5	0.92	1.0	0.45

Table A3.2. Analysis of presence or absence of Canada thistle (*Cirsium arvense* (L.) Scop.) in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	415	38	6.3	<0.0001
Error	24	143	6.0		
Total	35	558			
Zone Main Effect	2	3.1	1.6	0.26	0.77
Treatment Main Effect	3	348	116	20	<0.0001
Zone by Treatment Interaction	6	64	11	1.8	0.14

Table A3.3. Analysis of presence or absence of hound's tongue (*Cynoglossum officinale* L.) in various treatment and zone combinations in the ponderosa pine study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	11	183	17	2.3	0.046
Error	24	177	7.4		
Total	35	360			
Zone Main Effect	2	37	18	2.5	0.11
Treatment Main Effect	3	115	38	5.2	0.0066
Zone by Treatment Interaction	6	32	5.3	0.72	0.64

Appendix 4

Table A4.1. Analysis of American vetch (*Vicia Americana* Muhl. ex Willd.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	3.8	0.77	2.3	0.11
Error	12	4.0	0.33		
Total	17	7.8			
Zone Main Effect	1	1.8	1.8	5.4	0.038
Treatment Main Effect	2	0.63	0.31	0.94	0.42
Zone by Treatment Interaction	2	1.4	0.70	2.1	0.17

Table A4.2. Analysis of blue wildrye (*Elymus glaucus* Buckley) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	5.7	1.1	1.0	0.46
Error	12	13.65	1.1		
Total	17	19			
Zone Main Effect	1	0.46	0.46	0.41	0.54
Treatment Main Effect	2	4.2	2.1	1.9	0.20
Zone by Treatment Interaction	2	0.96	0.48	0.42	0.67

Table A4.3. Analysis of common dandelion (*Taraxacum officinale* F.H. Wigg.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	1.3	0.27	0.47	0.79
Error	12	6.8	0.57		
Total	17	8.1			
Zone Main Effect	1	0.85	0.85	1.5	0.24
Treatment Main Effect	2	0.29	0.14	0.25	0.78
Zone by Treatment Interaction	2	0.19	0.094	0.17	0.85

Table A4.4. Analysis of common gaillardia (*Gaillardia aristata* Pursh) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	0.72	0.14	6.7	0.0033

Error	12	0.26	0.022		
Total	17	0.98			
Zone Main Effect	1	0.0048	0.0048	0.22	0.65
Treatment Main Effect	2	0.71	0.35	17	0.0004
Zone by Treatment Interaction	2	0.0095	0.0048	0.22	0.80

Table A4.5. Analysis of common yarrow (*Achillea millefolium* L.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	1.1	0.23	2.2	0.13
Error	12	1.3	0.11		
Total	17	2.4			
Zone Main Effect	1	0.093	0.093	0.88	0.37
Treatment Main Effect	2	0.58	0.29	2.7	0.11
Zone by Treatment Interaction	2	0.47	0.24	2.2	0.15

Table A4.6. Analysis of cream pea (*Lathyrus ochroleucus* Hook.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	1.0	0.20	0.56	0.73
Error	12	4.4	0.36		
Total	17	5.4			
Zone Main Effect	1	0.27	0.27	0.74	0.41
Treatment Main Effect	2	0.10	0.052	0.14	0.87
Zone by Treatment Interaction	2	0.65	0.32	0.89	0.44

Table A4.7. Analysis of flexile milkvetch (*Astragalus flexuosus* Douglas ex G. Don) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	1.3	0.26	0.48	0.79
Error	12	6.4	5.3		
Total	17	7.7			
Zone Main Effect	1	0.97	0.97	1.8	0.20
Treatment Main Effect	2	0.11	0.056	0.10	0.90
Zone by Treatment Interaction	2	0.20	0.098	0.18	0.84

Table A4.8. Analysis of fowl bluegrass (*Poa palustris* L.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	1.4	0.28	0.78	0.58
Error	12	4.3	0.36		
Total	17	5.7			
Zone Main Effect	1	0.0054	0.0054	0.02	0.90
Treatment Main Effect	2	0.017	0.0086	0.02	0.98
Zone by Treatment Interaction	2	1.4	0.69	1.9	0.19

Table A4.9. Analysis of Gunnison's mariposa lily (*Calochortus gunnisonii* S. Watson) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	0.093	0.019	5.3	0.0088
Error	12	0.043	0.0036		
Total	17	0.14			
Zone Main Effect	1	0.014	0.014	4.0	0.069
Treatment Main Effect	2	0.069	0.034	9.7	0.0031
Zone by Treatment Interaction	2	0.010	0.0050	1.4	0.28

Table A4.10. Analysis of Kentucky bluegrass (*Poa pratensis* L.) canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	3.8	0.76	0.33	0.89
Error	12	28	2.3		
Total	17	32			
Zone Main Effect	1	0.48	0.48	0.21	0.66
Treatment Main Effect	2	0.49	0.24	0.11	0.90
Zone by Treatment Interaction	2	2.9	1.4	0.62	0.56

Table A4.11. Analysis of kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	6.1	1.2	0.78	0.59
Error	12	19	1.6		
Total	17	25			

Zone Main Effect	1	0.93	0.93	0.58	0.46
Treatment Main Effect	2	2.3	1.2	0.72	0.51
Zone by Treatment Interaction	2	2.9	1.4	0.90	0.43

Table A4.12. Analysis of limber honeysuckle (*Lonicera dioica* L. var. *glaucescens* (Rydb.) Butters) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	5.1	1.0	2.0	0.15
Error	12	6.0	0.50		
Total	17	11			
Zone Main Effect	1	0.22	0.22	0.45	0.52
Treatment Main Effect	2	4.5	2.2	4.5	0.036
Zone by Treatment Interaction	2	0.40	0.20	0.40	0.68

Table A4.13. Analysis of meadow zizia (*Zizia aptera* (A. Gray) Fernald) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	0.20	0.040	0.07	1.0
Error	12	7.0	0.58		
Total	17	7.2			
Zone Main Effect	1	0.00079	0.00079	0.00	0.97
Treatment Main Effect	2	0.078	0.039	0.07	0.94
Zone by Treatment Interaction	2	0.12	0.061	0.10	0.90

Table A4.14. Analysis of mountain brome (*Bromus marginatus* Nees ex Steud.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	0.61	0.12	2.0	0.15
Error	12	.73	0.061		
Total	17	1.3			
Zone Main Effect	1	0.080	0.080	1.3	0.28
Treatment Main Effect	2	0.41	0.21	3.4	0.069
Zone by Treatment Interaction	2	0.12	0.060	0.98	0.41

Table A4.15. Analysis of northern bedstraw (*Galium boreale* L.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	0.43	0.086	0.80	0.57
Error	12	1.3	0.11		
Total	17	1.7			
Zone Main Effect	1	0.019	0.019	0.18	0.68
Treatment Main Effect	2	0.17	0.085	0.79	0.48
Zone by Treatment Interaction	2	0.24	0.12	1.12	0.36

Table A4.16. Analysis of purple meadowrue (*Thalictrum dasycarpum* Fisch. & Avé-Lall.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	8.3	1.7	3.9	0.024
Error	12	5.1	0.42		
Total	17	13.4			
Zone Main Effect	1	0.012	0.012	0.03	0.87
Treatment Main Effect	2	8.0	4.0	9.4	0.0035
Zone by Treatment Interaction	2	0.30	0.15	0.35	0.71

Table A4.17. Analysis of quacking aspen (*Populus tremuloides* Michx.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	40	7.9	2.6	0.081
Error	12	37	3.0		
Total	17	77			
Zone Main Effect	1	30	30	10	0.0082
Treatment Main Effect	2	6.8	3.4	1.1	0.36
Zone by Treatment Interaction	2	2.4	1.2	0.39	0.69

Table A4.18. Analysis of Richardson's needlegrass (*Achnatherum richardsonii* (Link) Barkworth) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	0.97	0.19	0.57	0.72
Error	12	4.1	0.34		
Total	17	5.1			
Zone Main Effect	1	0.00039	0.00039	0.00	0.97
Treatment Main Effect	2	0.30	0.15	0.44	0.65
Zone by Treatment Interaction	2	0.67	0.34	1.0	0.40

Table A4.19. Analysis of rough bluegrass (*Poa trivialis* L.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	18	3.6	1.8	0.19
Error	12	24	2.0		
Total	17	42			
Zone Main Effect	1	5.2	5.2	2.6	0.13
Treatment Main Effect	2	9.0	4.5	2.2	0.15
Zone by Treatment Interaction	2	3.8	1.9	00.93	0.42

Table A4.20. Analysis of silvery lupine (*Lupinus argenteus* Pursh) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	2.3	0.46	0.67	0.65
Error	12	8.2	0.68		
Total	17	11			
Zone Main Effect	1	0.0083	0.0083	0.01	0.91
Treatment Main Effect	2	2.2	1.1	1.6	0.24
Zone by Treatment Interaction	2	0.087	0.043	0.06	0.94

Table A4.21. Analysis of slender cinquefoil (*Potentilla gracilis* Douglas ex Hook.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	4.3	0.86	2.1	0.14
Error	12	5.0	0.42		
Total	17	9.3			
Zone Main Effect	1	0.16	0.16	0.39	0.55
Treatment Main Effect	2	3.5	1.7	4.2	0.042
Zone by Treatment Interaction	2	0.66	0.33	0.79	0.48

Table A4.22. Analysis of slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinners ssp. *subsecundus* (Link) A. Löve & D. Löve) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	0.70	0.14	3.7	0.030
Error	12	0.46	0.08		

Total	17	1.2			
Zone Main Effect	1	0.11	0.11	2.8	0.12
Treatment Main Effect	2	0.53	0.27	7.0	0.0098
Zone by Treatment Interaction	2	0.061	0.031	0.81	0.47

Table A4.23. Analysis of sticky purple geranium (*Geranium viscosissimum* Fisch. & C.A. Mey. ex C.A. Mey.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	3.6	0.73	2.1	0.14
Error	12	4.2	0.35		
Total	17	7.8			
Zone Main Effect	1	0.78	0.78	2.3	0.16
Treatment Main Effect	2	0.90	0.45	1.3	0.31
Zone by Treatment Interaction	2	1.9	0.97	2.8	0.10

Table A4.24. Analysis of Virginia strawberry (*Fragaria virginiana* Duchesne) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	1.4	0.28	0.74	0.61
Error	12	4.5	0.37		
Total	17	5.9			
Zone Main Effect	1	0.0010	0.0010	0.00	0.96
Treatment Main Effect	2	1.3	0.63	1.7	0.22
Zone by Treatment Interaction	2	0.11	0.057	0.15	0.86

Table A4.25. Analysis of western snowberry (*Symphoricarpos occidentalis* Hook.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	5.3	1.1	1.1	0.41
Error	12	12	0.97		
Total	17	17			
Zone Main Effect	1	0.089	0.089	0.09	0.77
Treatment Main Effect	2	3.5	1.7	1.8	0.21
Zone by Treatment Interaction	2	1.8	0.88	0.91	0.43

Table A4.26. Analysis of white clover (*Trifolium repens* L.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	9.8	2.0	1.4	0.29
Error	12	16.7	1.4		
Total	17	27			
Zone Main Effect	1	1.5	1.5	1.1	0.32
Treatment Main Effect	2	7.3	3.7	2.6	0.11
Zone by Treatment Interaction	2	0.96	0.48	0.35	0.71

Table A4.27. Analysis of Woods' rose (*Rosa woodsii* Lindl.) percent canopy cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	0.33	0.066	0.10	0.99
Error	12	7.7	0.64		
Total	17	8.0			
Zone Main Effect	1	0.053	0.053	0.08	0.78
Treatment Main Effect	2	0.085	0.042	0.07	0.94
Zone by Treatment Interaction	2	0.19	0.096	0.15	0.86

Table A4.28. Analysis of Bare ground percent cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	7.6	1.5	2.2	0.13
Error	12	8.4	0.70		
Total	17	16			
Zone Main Effect	1	0.65	0.65	0.93	0.35
Treatment Main Effect	2	5.6	2.8	4.0	0.046
Zone by Treatment Interaction	2	1.3	0.66	0.94	0.42

Table A4.29. Analysis of Litter percent cover in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	1.3	0.26	1.2	0.37
Error	12	2.6	0.22		
Total	17	3.9			
Zone Main Effect	1	1.1	1.1	5.0	0.046
Treatment Main Effect	2	0.12	0.058	0.27	0.77
Zone by Treatment Interaction	2	0.11	0.053	0.25	0.79

Appendix 5

Table A5.1. Analysis of present canopy cover of grasses in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	2.1	0.42	0.28	0.91
Error	12	18	1.5		
Total	17	20			
Zone Main Effect	1	0.41	0.41	0.27	0.61
Treatment Main Effect	2	0.039	0.020	0.01	0.99
Zone by Treatment Interaction	2	1.7	0.83	0.55	0.59

Table A5.2. Analysis of present canopy cover of forbs in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	6.7	1.3	5.6	0.0067
Error	12	2.8	0.24		
Total	17	9.5			
Zone Main Effect	1	0.050	0.050	0.21	0.65
Treatment Main Effect	2	4.3	2.2	9.1	0.0040
Zone by Treatment Interaction	2	2.3	1.2	4.9	0.028

Table A5.3. Analysis of present canopy cover of shrubs in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	5.4	1.1	0.57	0.72
Error	12	23	1.9		
Total	17	28			
Zone Main Effect	1	0.076	0.076	0.04	0.85
Treatment Main Effect	2	2.1	1.1	0.55	0.59
Zone by Treatment Interaction	2	3.2	1.6	0.85	0.45

Appendix 6

Table A6.1. Analysis of presence or absence of Canada thistle (*Cirsium arvense* (L.) Scop.) in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	80	16	1.7	0.21
Error	12	114	9.5		
Total	17	194			
Zone Main Effect	1	1.5	1.5	0.16	0.70
Treatment Main Effect	2	73	36	3.8	0.052
Zone by Treatment Interaction	2	5.5	2.8	0.29	0.75

Table A6.2. Analysis of presence or absence of hound's tongue (*Cynoglossum officinale* L.) in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	24	4.7	0.43	0.82
Error	12	132	11		
Total	17	156			
Zone Main Effect	1	0.32	0.32	0.03	0.87
Treatment Main Effect	2	16	8.1	0.74	0.50
Zone by Treatment Interaction	2	7.1	3.5	0.32	0.73

Table A6.3. Analysis of presence or absence of meadow thistle (*Cirsium scariosum* Nutt.) in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	54	11	2.3	0.11
Error	12	57	4.7		
Total	17	111			
Zone Main Effect	1	3.7	3.7	0.77	0.40
Treatment Main Effect	2	43	21	4.5	0.035
Zone by Treatment Interaction	2	7.3	3.7	0.77	0.48

Table A6.4. Analysis of presence or absence of nodding plumeless thistle/musk thistle (*Carduus nutans* L.) in various treatment and zone combinations in the aspen study sites of the Jasper fire within the Black Hills National Forest, South Dakota, U.S.A.

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Source	DF	Sum of Squares	Mean Squares	F-value	P
Model	5	9.2	1.8	1.0	0.46
Error	12	22	1.8		
Total	17	31			
Zone Main Effect	1	1.8	1.8	1.0	0.34
Treatment Main Effect	2	3.7	1.8	1.0	0.40
Zone by Treatment Interaction	2	3.7	1.8	1.0	0.40