DISSERTATION

CHANGES IN FOREST STRUCTURE, COMMUNITY COMPOSITION, AND DEVELOPMENT IN PONDEROSA PINE FORESTS FOLLOWING A MIXED-SEVERITY WILDFIRE IN THE BLACK HILLS, SD, USA.

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY TARA LYNN KEYSER ENTITLED CHANGES IN FOREST STRUCTURE, COMMUNITY COMPOSITION, AND DEVELOPMENT IN PONDEROSA PINE FORESTS FOLLOWING A MIXED-SEVERITY WILDFIRE IN THE BLACK HILLS, SD, USA BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

CHANGES IN FOREST STRUCTURE, COMMUNITY COMPOSITION, AND DEVELOPMENT IN PONDEROSA PINE FORESTS FOLLOWING A MIXED-SEVERITY WILDFIRE IN THE BLACK HILLS, SD, USA.

Fire behavior in ponderosa pine (*Pinus ponderosa* Laws.) forests of the interior West can vary along a continuum from low severity surface fire to high severity crown fire. Variations in fire behavior differentially impact forest vegetation and create a fine-scale mosaic of low, moderate, and high severity fire effects across the landscape. The immediate and longer-term impact mixed-severity wildfires have on forest overstory and understory structure and composition vary greatly in relation to fire severity and are not well understood. Here, we describe the long-term implications of the Jasper fire on overstory and understory forest development.

In stands where low severity fire occurred, the fire had little impact on the structure of the overstory and understory vegetation. However, it did cause significant reductions in the forest floor litter and woody fuel layer reducing future fire hazard and potential fire severity. In contrast, stands impacted by moderate severity fire, resulting from passive crown fire, experienced significant changes throughout the forest overstory, understory, and forest floor. Substantial reductions in overstory tree density created an open, park-like stand with a grass/forb dominated understory that will persist until tree regeneration, recruitment, and canopy closure

once again occurs. High rates of mortality, however lead to significant build-up of hazardous fuel which may increase future fire hazard and potential fire severity. Finally, stands impacted by high severity fire, which resulted from active, stand-replacing crown fire, led to a long-term change in cover type from a closed-canopied ponderosa pine forest to a grass and forb dominated meadow. Even with no overstory, these stands will continue to be susceptible to high severity surface fire well into the future due to the build-up of hazardous fuels resulting from the rapid snag-fall of fire-killed trees.

While these mixed-severity wildfires are often viewed as catastrophic events, they are, in actuality, disturbance events that increase structural and compositional heterogeneity throughout an otherwise homogeneous landscape. In the case of the Black Hills where mixed-severity wildfires were part of the historic fire regime, recent mixed-severity wildfires actually restore many of the structural and compositional components present on the landscape prior to Euro-American settlement.

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I. INTRODUCTION

The immediate and long-term impacts of mixed-severity wildfire on postfire stand dynamics, ecological succession, and species composition of ponderosa pine (*Pinus ponderosa* Laws.) forests are poorly understood. Fire behavior in ponderosa pine forests can vary from low-intensity surface fire to high-intensity, active crown fire (Lentile et al. 2005, Fule' et al. 2003). The severity of direct fire effects and subsequent impacts on the forest vegetation, forest floor, understory community, and soil nitrgoen vary in congruence with these widespread variations in fire behavior. Vegetation that burns under low-intensity surface fire often experiences low levels of damage and mortality whereas vegetation that burns under high-intensity crown fire undergoes complete mortality. These variations in fire behavior and the severity of resultant fire effects are attributed to fine-scale differences in forest stand structure and topography (Lentile et al. 2006) as well as the quantity and continuity of fuels and weather conditions (Turner et al. 1994). The interactions among these controlling factors create situations where adjacent forest stands experience differing levels of fire behavior and severity making recovery to prefire conditions variable across the landscape.

In the low elevation forests of the southwestern United States, periodic low-intensity surface fires maintained open, park-like stands of ponderosa pine prior to Euro-American settlement (Covington and Moore 1994). Current restoration efforts and postfire rehabilitation prescriptions are often guided by the requirement or desire to restore the pre-Euro-American structure throughout the landscape. In the Southwest, the recent increase in mixed- or high-severity wildfires that have occurred since 2000 (e.g. Rodeo-Chediski fire) are considered detrimental to ecosystem structure, function, and composition. In other geographic areas, such as the Black Hills of South Dakota where historic fire regimes contained elements of low-intensity surface fire coupled with moderate-intensity passive crown fire and high-intensity, active crown fire, mixed-severity wildfires can restore elements of historic forest structure and greatly increase landscape heterogeneity (Battaglia 2007, Graves 1899).

The Black Hills is a heavily managed landscape consisting of a predominantly second-growth ponderosa pine forests. Along with recreation, timber is the primary commodity derived from the forest making it one of the most productive forests in the National Forest System in terms of volume harvested. In late August, 2000, the Jasper wildfire was ignited in the southwestern Black Hills. After 8 days, the Jasper fire had impacted ~34,000 ha or ~7% of the Black Hills National Forest (BHNF) land base, making it the largest wildfire in the Black Hills in recorded history (USDA 2000). Fire behavior during this single-event wildfire varied from low-intensity surface fire to high-intensity active crown fire.

Recent large-scale fires, including the Jasper fire, have burned predominantly within the BHNF timber base. Land-use management decisions regarding postfire rehabilitation efforts such as salvage logging that are intended to recover value from dead and dying trees (Lindenmayer et al. 2004) as well as reduce fuel loadings (McIver and Ottmar 2007) must be made within the immediate months following the fire for the trees to be of any economic value. While salvage operations can capture immediate and incipient mortality, practical and readily implemented guidelines regarding which trees to salvage are lacking. Many mortality models specific for ponderosa pine use variables such as ground char that are not easily measured in the field (e.g. Swezy and Agee 1991) whereas others fail to take into consideration fire effects such as cambial damage known to significantly impact tree mortality (e.g. Harrington 1993). In Chapter II, we develop an accurate and efficiently employed model to predict the 5-year mortality of ponderosa pine based on tree size and easily observed fire effects including crown and cambial damage with the goal being to increase the land manager's ability to discriminate between those trees that will die and those trees that will survive throughout the immediate 5 years following fire. This model will ultimately aid managers in making more science-based postfire management decisions and designing more ecologically sound salvage guidelines that minimize the removal of postfire survivors and lessen the ecological impacts that may be associated with salvage operations (e.g. Donato et al. 2006).

The economic and ecological costs of postfire rehabilitation and restoration efforts are staggering. The variation in fire effects and resultant changes in overstory and forest floor structure associated with mixed-severity fire creates a challenge for land managers charged with creating and implementing appropriate postfire management prescriptions. Postfire practices such as salvage logging, incorrectly applied, can increase future fire hazard and slow forest recovery and future development (Denato 2006). Aerial seeding operations designed to reduce postfire erosion often introduce and spread exotic and noxious herbaceous weeds at the expense of native species, thereby lowering biodiversity (Hunter et al. 2006). In Chapter III, we assess the immediate impact of low, moderate, and high severity fires on postfire stand dynamics of the overstory and forest floor. Areas that burned under low severity fire experienced little change in overstory structure limiting the impact on overall stand stocking and growth yet had significant reductions in forest floor mass and surface woody fuel loadings. In contrast, areas that burned under moderate severity fire experienced significant overstory and understory tree mortality that resulted in a rapid build-up of the postfire fuel bed. The presence of residual seed trees, however, ensures future regeneration and forest development. Areas of high severity fire experienced complete tree mortality which contributed to excess fuel build-up after 5 years and removed the ponderosa pine seed source making any chance of substantial ponderosa pine regeneration within these stands questionable. Due to the variability in direct and secondary fire effects, we conclude that postfire rehabilitation efforts, specifically salvage logging and artificial planting, need to vary across severities in these mixed-severity type fire events. Appropriate responses include small-scale, sometimes stand-level based mitigation measures ranging from no action in areas of low severity fire to more intensive actions such as artificial planting in high severity areas.

Finally, in chapter IV, we examine the impact of fire severity on changes in the structure and composition of the understory vegetation. Fire modifies understory species composition through the selective removal of non-fire resistant species (Agee 1993). However, numerous factors related to fire behavior and fire severity, including overstory tree mortality which increases canopy light transmittance, consumption of organic matter which increases nutrient availability and exposes bare mineral soil (DeBano et al. 1998), and reduced competition for water, nutrients, and light (Reigel et al. 1995) interact to influence the recovery of understory plant communities following fire. The increased landscape heterogeneity we observed in overstory and forest floor structure following the

Jasper fire was reflected within the understory community. We found that the shrub dominated forest stands that existed prior to the Jasper fire were not present at anytime during the 5 years following the fire. Instead, low, moderate, and high severity stands were dominated by forbs and grasses. Additionally, species composition diverged from unburned conditions, regardless of fire severity, throughout the 5 years following the fire. The diversity in species composition, in conjunction with a significant shift in functional group dominance suggests that community and cover types that were rare on the landscape prior to the Jasper fire now dominate this 34,000 ha landscape.

The immediate and perceived effects of mixed-severity wildfires on the landscape change over time. Overstory mortality, forest floor development, hazardous fuel build-up, and understory structure and composition vary with fire behavior and resultant fire effects as well as with time since fire. The results of these studies demonstrate how forest recovery and development varies within these single event wildfires. The perceptions that these fires are catastrophic events that homogenize the landscape were unrealized after the Jasper fire. The variability in fire effects that occurred within mixed-severity fire translated into a heterogeneous landscape with the magnitude of departure from prefire conditions dependent upon fire behavior and fire severity.

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II. MODELING POSTFIRE MORTALITY OF PONDEROSA PINE FOLLOWING A MIXED-SEVERITY WILDFIRE IN THE BLACK HILLS: THE ROLE OF TREE MORPHOLOGY AND DIRECT FIRE EFFECTS

ABSTRACT

We examined the relation between tree size, crown and stem damage and 5 years of postfire mortality of ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) in the Black Hills following a large, mixed-severity wildfire. We measured tree morphology and direct fire effects on 963 trees and assessed individual tree mortality annually from 2001-2005. We used logistic regression to model tree mortality as a function of tree morphology [diameter at breast height (DBH) and bark thickness (BARK)] and direct fire effects [percent of the live crown scorched (PSCOR) and basal char measured as the percentage of the bole charred below 30 cm (CHAR)]. Models using DBH and BARK were modeled separately due to correlation between the variables. In all models, mortality decreased with increasing DBH and BARK and increased with increasing PSCOR and CHAR. Basal char contributed to the mortality of trees less than 40 cm but became less influential as DBH and BARK increased. Overall, probability of mortality modeled as a function of DBH, PSCOR, and CHAR correctly predicted the status of 78% of trees whereas the model predicting mortality as a function of BARK, PSCOR, and CHAR had an increase in prediction accuracy of only 1%.

INTRODUCTION

The ability to accurately predict individual tree mortality following fire has important management implications. Whether a tree will live or die influences timber salvage operations which focus on removing trees immediately killed by fire or those trees that can be expected to die within a period of a few years following fire. The ability to predict postfire mortality provides managers insight into postfire forest structure and function and its relation to future timber production, changes in wildlife habitat, and long-term planning objectives. Decision-making criteria regarding postfire management operations need to be based on accurate and efficient postfire assessments. Of particular importance is information regarding delayed tree mortality as fire-killed trees are subject to insect and disease infestations (McHugh et al. 2003) rendering the timber unsalvageable. The issues and concerns over the potential ecological effects that postfire salvage operations have on forest recovery processes and future forest stand development (Donato et al. 2006, Purdon et al. 2004, Lindenmayer et al. 2004) along with the increased loss of timber from forests' timber base due to the increase in large-scale wildfires (Keegan et al. 2004) has emphasized the need to base postfire management decisions on accurate models of predicted postfire mortality. In this paper, we develop accurate and efficient models to predict the 5-year mortality of ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) based on tree morphology, in particular tree size and bark thickness, and observed fire effects following a large, mixed-severity wildfire in the Black Hills of South Dakota.

Individual tree mortality caused by fire is the result of direct heat or flame damage to the foliage (i.e. scorch and consumption), cambium, and root system which disrupts tree physiological processes such as water transport, nutrient uptake, and photosynthesis (Swezy and Agee 1991, Ryan and Reinhardt 1988, Ryan et al. 1988). Tree morphology, in particular tree diameter, bark thickness, crown base height, and foliage density (Ryan and Reinhardt 1988) and prefire tree vigor (van Mantgem et al. 2003) all play a significant role in estimating the resistance of individual trees and tree species to fire-related injury and death. Diameter at breast height (DBH) and bark thickness impact the resistance of a tree to cambial injury and girdling (Vines 1968) while crown base height and foliage density influence the severity and degree of crown injury that directly affect bud survival and new shoot production, as well as postfire photosynthetic capacity (Wyant et al. 1983).

The most important factor influencing postfire tree mortality is crown injury. Recent mortality studies have focused on the percentage of crown volume killed either by scorch and (or) consumption as an indicator of crown damage (McHugh and Kolb 2003, Stephens and Finney 2002, Ryan and Reinhardt 1988). Many species are able to withstand moderate to extreme levels of crown damage without experiencing increased mortality rates. McHugh and Kolb (2003) found following wildfire in northern Arizona, mortality for ponderosa pine did not begin until 70% of the total crown volume was damaged while Stephens and Finney (2002) report giant sequoia (*Seqoiadendron giganteun* [Lindley] Buchholz) was able to withstand 90% total crown volume damage before mortality occurred following prescribed fire in central California. These results suggest the amount of crown damage an individual tree can withstand is species specific. Regardless of species, however, there are no studies that report high rates of mortality at levels of crown damage below 10% (Stephens and Finney 2002).

Stem damage has also been shown to be an important predictor of postfire mortality (McHugh and Kolb 2003, Peterson and Arbaugh 1989, 1986). Ryan et al. (1988) found that the amount of dead cambium at 1.4 m was the most important predictor of postfire mortality for Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) following light surface fire in Montana while numerous other studies report that cambial damage describes a significant amount of variability in mortality models second in importance, however, to crown damage (e.g. Peterson and Arbuagh 1989, 1986, Wyant et al. 1986). Tree mortality is often lower for trees with larger DBH and greater bark thickness compared to smaller trees (Hély et al. 2003, Borchert et al. 2002, Regelbrugge and Conard 1993, Ryan and Reinhardt 1988). Increased DBH and subsequently increased bark thickness (van Mantgem and Schwartz 2003) insulate cambial tissue from the heat flux from fire. Bark scorch/char measurements taken as bark char ratio (depth of char/bark thickness) (Peterson and Arbaugh 1989, 1986) and height of bole scorch/char (Wyant et al. 1986) are often used as a surrogate for stem and cambial damage in many models. No single predictor provides an accurate estimate of postfire mortality; rather a combination of crown and stem damage and morphology most accurately predict mortality. Current published tree mortality models often seek to explain the underlying physiological processes of postfire mortality rather than use variables that can be easily or efficiently applied to the field and salvage marking operations.

Ponderosa pine is the dominant tree species in the Black Hills of South Dakota and occupies an estimated 85% of the landscape (Deblander 2002). Ponderosa pine is also the single-most valuable timber species in the Black Hills. In recent years, more frequent, large-scale fires have occurred resulting in substantial losses of standing timber.

Between 2000 and 2004, seven fires have burned ~60,000 ha of ponderosa pine dominated forests in the Black Hills (Lentile 2004). Mortality models that can accurately predict the future status of fire-injured trees by measuring fire effects on the crown as well as stem helps to ensure that only those trees likely to die within the years following wildfire are salvaged and any potentially live trees will be reserved and left to influence postfire recovery processes such as postfire regeneration. The Jasper fire and the subsequent long term monitoring of postfire recovery processes has provided a unique opportunity to observe how wildfire impacts postfire mortality of ponderosa pine in the Black Hills. The objective of this study was to develop an accurate model of postfire mortality for ponderosa pine in the Black Hills. Specifically, we used long-term monitoring data to (*i*) evaluate the role crown and bole damage has in conjunction with tree size and bark thickness in predicting postfire mortality, (*ii*) discuss the potential physiological relationships between mortality and the predictive variables, and (*iii*) provide an efficient, predictive mortality model that can be used in postfire management decision making processes regarding ponderosa pine in the Black Hills.

METHODS

Study area

This study was conducted within the Black Hills National Forest, South Dakota, USA. The Black Hills are an isolated, forested uplift on the Missouri Plateau of the Great Plains Province (Hoffman and Alexander 1987) and form the easternmost extent of the Rocky Mountains (Froiland 1990). In late August, 2000, the Jasper fire was ignited near Custer, SD in the southwestern Black Hills. The Jasper fire burned ~34,000 ha of the

Limestone Plateau area of the Black Hills (Shepperd and Battaglia 2002, USDA Forest Service http://www.fs.fed.us/r2/blackhills/fire/history/jasper/00_11_09_JRAT_Report.pdf. October 15, 2005). Elevations within the burn area range from ~1,500 to 2,100 m. The fire was a mixed-severity fire producing a combination of surface fire (low fire behavior), surface fire with torching (moderate fire behavior), and active crown fire (extreme fire behavior) that burned through predominantly ponderosa pine forest leaving behind a mosaic of low, moderate, and high severity fire effects across the landscape (USDA Forest Service http://www.fs.fed.us/r2/blackhills/fire/history/jasper/00_11_09_JRAT_Report.pdf. October 15, 2005; Lentile et al. 2005). Dominant soil types are similar within the fire perimeter and consist of Alfisols, Mollisols, and Inceptisols (Shepperd and Battaglia 2002). Annual precipitation averages from 45 to 48 cm with between 60 and 73% of the annual precipitation falling from April to September (Hoffman and Alexander 1987). Mean daily minimum and maximum temperatures are -3.3 and 13.2° C.

Methods

In June 2001, prior to the fall of fire-scorched needles, we established 18 – ~0.3 ha permanent study sites in ponderosa pine stands within the Jasper fire perimeter. Within these burned stands, 9 sites were located in areas exhibiting evidence of surface fire behavior with low initial postfire tree mortality and 9 sites were located in ponderosa pine stands exhibiting moderate fire behavior consisting of surface fire with individual tree torching resulting in moderate initial postfire tree mortality. Each site consisted of 3 – 0.03 ha plots. Plots were located at bearings 0°, 135°, and 225° azimuth 20 m from site center. Study sites were similar in respect to species composition, aspect, slope (5-13%), elevation, and soil type.

Within each plot, we tagged every tree ≥1.4 cm DBH, recorded species, and assessed tree mortality annually from 2001 to 2005. Trees with no green foliage were considered dead. We measured tree morphology including bole diameter taken at 1.4 m above the soil surface (DBH) and bark thickness. Bark thickness was sampled at DBH at two different locations on the bole so an average bark thickness per tree could be computed (BARK). In addition, we measured total tree height (HT) and prefire crown base height (CBH). Crown base height was measured at the point of branch-bole attachment of the lowest prefire live whorl. We identified prefire crown base height from the position of scorched needles in the case where no foliage consumption occurred and fine branch structure in the case where consumption of needles occurred. Scorched needles were easily distinguishable from non-scorched needles as they were brown or orange in color. Crown injury was measured on individual trees and included maximum height of crown scorch (MAXSCOR) which was measured as the maximum height on the crown where necrotic foliage occurred. Foliage necrosis due to crown scorch is caused when the foliage experiences lethal temperatures as a direct result of radiant heat or direct flame produced by the flaming front of the fire (Johnson and Miyanishi 2001). We measured the percentage of the bole circumference charred below 30 cm (CHAR) to the nearest 5% as an indicator of stem and cambial damage. Charred bark was distinguished from scorched bark as it was metallic black in color (similar to the color and texture of charcoal) and was eroded to the point the bark no longer contained grooves or furrows whereas scorched bark was completely intact and black or gray in color (Lentile 2004).

We calculated an additional fire effects variable, percent of live crown length scorched (PSCOR) which was calculated as:

[(MAXSCOR-CBH)/(HT-CBH)]*100

Data analysis

Only trees ≥5 cm DBH were included in the data analysis. We conducted Wilcoxon rank sum tests in order to determine if prefire stand structure differed between areas of low and moderate postfire mortality ($\alpha = 0.05$). We also tested if tree size and bark thickness as well as the severity of direct fire effects differed among live trees and trees that died within a given year as well as at the end of 5 years. We used logistic regression to model the probability of tree mortality five years postfire. Numerous studies (e.g. Stephens and Finney 2002, Regelbrugge and Conard 1993, Ryan and Reinhardt 1988) have used logistic regression to effectively model postfire tree mortality. The logistic model has the form:

$$P(m) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n)}}$$

where P(m) is the probability of mortality, β_0 through βn are the model coefficients, and X_1 through X_n are the explanatory variables. Mortality data is categorical with a binary outcome (Peng et al. 2002); 0=live or 1=dead. The logistic function provides a continuous estimate of the probability of mortality between 0 and 1. We used the standard cutoff of 0.5 to signal mortality (Saveland and Neuenschwander 1990). Therefore, when $P_m<0.5$, the tree is predicted live and when $P_m>0.5$, the tree is predicted dead.

We used DBH, BARK, PSCOR, and CHAR as well as the appropriate interactions as independent variables to predict the 5-year mortality of ponderosa pine. Unless specified, interactions among independent variables were not significant ($P >$ 0.05) and therefore not included in the final models. Due to the high correlation between DBH and bark thickness (r=0.70), separate models were created using these two variables. All other variables were uncorrelated with one another (r<0.50). Models were built using a random sample of ~75% of the full dataset [calibration dataset (n=722 for models using DBH and n=721 for models using BARK)]. To test the predictability of the model, we ran validation runs on the remaining ~25% of the full dataset [validation dataset (n=241)]. All analyses were performed using SAS version 9.1. We used a maximum likelihood fitting procedure (Cook and Weisberg 1999) using SAS LOGISTIC to estimate model coefficients (SAS Institute 1989). We used the generalized Wald statistic with a χ^2 distribution to test if model coefficients were different from 0 (α=0.05). Asymptotic confidence intervals based on the profile likelihood procedure were calculated for all regression coefficients and provide an understanding of how precisely the coefficients were estimated. Model goodness-of-fit was assessed using the Hosmer-Lemeshow goodness-of-fit statistic (α=0.05; Hosmer and Lemeshow 2002) and receiver operations characteristic (ROC) curve analysis (Hosmer and Lemeshow 2000, Saveland and Neuenschwander 1990). The ROC curve is a plot of the sensitivity vs. (1-specificity) of the model where sensitivity is equal to the probability of detecting a true event and (1-specificity) is equal to the probability a predicting a false event over the entire range (0 to 1) of cutoff points (Hosmer and Lemeshow 2000). Models with ROC values $\geq$ 0.7 are considered to have an acceptable discrimination between live and dead trees, ROC values

≥ 0.8 have excellent discrimination, and ROC values ≥ 0.9 are considered to have outstanding discrimination (Hosmer and Lemeshow 2000). Nested models were compared against each other based on the likelihood ratio test where the $Pr(\chi^2>G) = -2$ Log Likelihood value (-2LL) of the full model – -2LL value of the reduced model with $df = df_{\text{full model}} - df_{\text{reduced model}}$.

RESULTS

Prefire stand structure including density and average stand diameter was similar between areas that experienced low and moderate levels of fire behavior suggesting that sites were similar enough in stand structure to be modeled together ($P > 0.05$). Study sites had an average ponderosa pine density of 594 trees ha^{-1} with an average stand diameter of ~23 cm.

Postfire ponderosa pine mortality differed among all 5 years of the study although most mortality occurred between 2001 and 2003 (Fig. 2.1). The number of trees dying in a single year peaked in 2002 with 93 trees ha^{-1} dying within the year. Mortality declined slightly in 2003 and was negligible by 2005 when the equivalent of only 7 trees ha^{-1} were identified as having died from the previous year. Eighty nine percent of the mortality in low and moderate severities occurred by the end of 2003 with the remaining 11% mortality occurring the following 2 years.

Five years postfire, tree morphology differed between live and dead trees (Fig. 2.2). Trees that died in years 2001-2003, were smaller in DBH than live trees ($P < 0.05$); however differences in DBH between surviving trees and trees that died in 2004 and 2005 were undistinguishable ($P > 0.05$). Throughout all five years, dead trees had significantly thinner bark than surviving trees ($P < 0.05$). Fire effects were also different between live and dead trees with dead trees possessing a significantly greater percentage of crown and stem damage throughout all five years of the study ($P < 0.05$). Crown damage was greatest in trees that died between 2000 and 2001, when PSCOR of a dead tree averaged 100%. In contrast, stem damage was greatest in trees that died between 2001 and 2002 when CHAR averaged 38%.

Using the model calibration dataset, a total of 8 univariate and multivariate logistic regression models were created (Table 2.1). Models 1 through 4 describe postfire mortality as a function of DBH while models 5 through 8 describe postfire mortality as a function of BARK. We included site as a variable in all models during the initial analysis to determine if differences among sites accounted for any significant variability in the ability to predict postfire mortality. In all eight models, site was not a significant variable ($P > 0.05$) suggesting that mortality was independent of site location.

Model 1, which is the univariate model using DBH as a predictor of mortality was a significant predictor of postfire mortality (ROC=0.70). Univariate models were produced because they are the simplest and most time efficient models to use; however they often do not explain enough variability in postfire mortality to provide an accurate estimate of the probability of mortality. While model 1 accounts for significant variability, the ROC value was at the threshold of the acceptable level of discrimination preferred in logistic regression analysis. Multivariate models that incorporated variables describing fire damage to the crown and stem significantly improved the model. Model 2 was initially tested as a 2-variable model predicting mortality as a function of DBH and PSCOR. However, further analysis indicated a significant interaction between these two variables. Therefore, model 2 was produced as a 3-variable model using DBH and included PSCOR and the significant interaction between DBH and PSCOR as predictors of mortality. The inclusion of PSCOR and the interaction between DBH and PSCOR explained significantly more variation in postfire mortality than did model 1 and had an acceptable level of discrimination between live and dead trees (G=141.1, df=2, $P <$ 0.0001, ROC=0.82). While a significant improvement over model 1, model 3 which calculates mortality as a function of DBH and CHAR did not explain as much variability in postfire mortality as did model 2 suggesting that CHAR in conjunction with DBH is not as strong of a predictor of mortality as PSCOR and the interaction between PSCOR and DBH. Based on -2LL and ROC values, the best logistic equation modeling postfire mortality as a function of DBH was model 4. Model 4 was the 3-variable model using the combination of DBH, PSCOR, and CHAR as significant predictors of mortality. In conjunction with CHAR, the interaction between DBH and PSCOR that existed in model 2 was no longer significant ($P > 0.05$). The addition of CHAR to the mortality model explained significantly more variability in the ability to predict postfire mortality than model 2 [-2LL=724.0, ROC=0.83 for (4) vs. -2LL=757.9, ROC=0.82 for (2)].

Overall, the models using BARK as the morphological predictor of mortality explained substantially more variation in postfire mortality than did the models that used DBH based on the ROC values. Model 5, which is the univariate model using BARK as a predictor of mortality, explained significantly more variation in postfire mortality than did model 1 [ROC=0.80 for (5) vs. ROC=0.70 for (1)]; however the Hosmer-Lemeshow test showed a significant lack-of-fit of model 5 to the calibration data (P=0.036). As with the multivariate models containing DBH, significant improvement in model fit and predictability occurred when fire effects variables were incorporated into the model. Model 6 was the best 2-variable model using BARK and included PSCOR as a predictor of mortality. Model 6 was a better model and predictor of mortality than BARK alone producing a lower -2LL value and greater ROC value (G=72.8, df=1, $P < 0.0001$, ROC=0.84). The best model using BARK as a predictor of mortality, however, was model 8 which was the 3-variable model predicting postfire mortality as a function of BARK, PSCOR, and CHAR. The addition of CHAR to model 6, which was the best 2-variable model, resulted in a significant increase in model performance and ability to predict mortality (G=27.7, df=1, $P < 0.0001$, ROC=0.86).

In all models, the coefficient for DBH and BARK was negative suggesting that an increase in DBH or BARK results in a significant decrease in the predicted probability of mortality. In contrast, coefficients for PSCOR and CHAR in all 8 models were positive suggesting that any increase in PSCOR and (or) CHAR results in a significant increase in the probability of mortality. At similar levels of CHAR, larger trees and trees with thicker bark were less susceptible to fire induced mortality than smaller trees and trees with thinner bark at comparable levels of PSCOR (Fig. 2.3). Increased predicted mortality associated with increasing levels of CHAR was most visible on small trees less than 30 cm DBH. These trees possessed a substantially higher predicted probability of mortality with CHAR levels of 75% versus only 25% (Fig. 2.3). In contrast, when CHAR was used in combination with bark thickness at comparable levels of PSCOR, the predicted probability of mortality was less sensitive to increases in CHAR. Trees with bark thickness of 2 cm and greater did not experience large increases in the predicted probability of mortality with increases in CHAR (Fig. 2.3).

Model validation

Model validation was performed using the model coefficients from the best model containing DBH (model 4, Table 2) and the best model containing BARK (model 8; Table 2.2). Model 4 accurately predicted the status of 189 observations producing an overall accuracy rate of 78%. Model 4 was better at predicting survival rather than mortality, correctly predicting the status of 84% of the live trees versus only 71% of the dead trees. Model 4, therefore, failed to detect 29% of the observed mortality in the test data and misclassified 16% of the observed live trees as dead. Model 8, which had better statistical properties than model 4, accurately predicted the status of 79% of the observations. Model 8 was better at predicting survival rather than mortality, correctly predicting 86% of the live trees versus 71% of the dead trees. Model 8 failed to detect 29% of observed mortality in the test data and misclassified 14% of the live trees in the test data as dead.

DISCUSSION

Mortality models

The goal of this study was to model long-term postfire mortality of ponderosa pine following a large, mixed-severity wildfire in the Black Hills. We focused on direct measurements of crown damage (PSCOR) and indirect measurements of cambial damage (CHAR) along with tree morphological characteristics that have been shown to influence postfire survival (DBH and BARK) as predictors of postfire mortality. Tree size is important because it influences a tree's susceptibility, resistance, and ability to survive both wildfire and prescribed fire while direct fire effects impact postfire physiological processes. We found that ponderosa pine mortality occurred throughout all five years of the study with the majority of postfire mortality occurring between 2001 and 2003 (Fig. 2.1). Data from this study relating tree mortality to time since fire are consistent with numerous other long-term studies (Agee 2003, Mutch and Parsons 1998, Ryan et al. 1988) that report high mortality within the first 2-4 years postfire followed by a dramatic decrease in mortality in the later postfire years.

Tree size was found to be an important variable for predicting postfire mortality. In model 4, we found that the predicted probability of mortality decreased with increases in DBH confirming other studies (Hély et al. 2003, Stephens and Finney 2002, Borchert et al. 2002, Regelbrugge and Conard 1993) that suggest that as tree diameter increases, the probability of mortality decreases. Tree diameter is positively related to bark thickness (van Mantgem and Schwartz 2003); therefore, DBH should provide a reliable estimate of resistance to cambium injury from fire as the corky bark often found in ponderosa pine insulates the cambium from the heat flux of a surface fire preventing full or partial girdling (Hare 1965). In addition to resistance to stem damage, tree size has implications on the severity of crown damage a tree sustains in a wildfire. Smaller trees have lower crown base heights than larger trees. Low crown base height often facilitates the transition of fire from the surface into the canopy.

In model 4, which predicted mortality as a function of DBH, crown, and stem damage, PSCOR was a significant variable for predicting postfire mortality. We measured crown damage using PSCOR which included the percent of the live crown length consumed as well as scorched. Needle scorch occurs when either direct or indirect heat kills crown foliage (Harrington 1987). Depending upon scorch height and crown length, this can have significant impacts on postfire photosynthetic production and recovery. Needles in the middle and lower third of ponderosa pine crowns produce significantly less photosynthate than is produced in the upper third of the crown (Ryan 1998, Assman 1970). Consequently, low mortality is associated with low values of PSCOR as the inefficient portions of the canopy are removed; however as PSCOR increases, especially as scorch height approaches the most phytosynthetically active and productive upper third of the canopy, increased mortality is observed.

We found that the predicted probability of mortality increased as PSCOR increased, especially in trees less than 30 cm DBH (Fig. 2.3). Regardless of CHAR levels, model 4 predicted survival of large trees even with 100% PSCOR. This is likely due to the fact that we used the percent of the crown length scorched whereas other studies have used the proportion of the total crown scorched and (or) consumed (McHugh and Kolb 2003, Saveland and Neuenschwander 1990, Wyant et al. 1986) which is a more accurate, but more time consuming measurement of crown damage taking into consideration the volume of needles and buds killed, not just the crown length killed. At low levels of CHAR (25%), we found that trees with a DBH of 10 cm can sustain only ~20% PSCOR before mortality occurs whereas trees with a DBH of 20 cm can withstand a maximum of ~70% PSCOR before mortality occurs (Fig. 2.3). This is consistent with results from Harrington (1987) who found crown scorch thresholds upwards of 90% for larger ponderosa pine in western Montana. In contrast, mortality of trees greater than 30 cm DBH were not impacted by PSCOR in combination with low levels of CHAR.

Similar to Peterson and Arbaugh (1986) who found that the proportion of the basal circumference charred was significant in predicting postfire mortality of lodgepole pine (*Pinus contorta* Dougl.), we found that including CHAR as a predictor of mortality for ponderosa pine greatly improved model fit and discrimination (Table 2.1). Cambium damage is greater and more damaging at the base of the tree than at breast height or above (Ryan 1990). Variables such as bark char ratio for Douglas-fir and lodgepole pine (Peterson and Arbaugh 1989, 1986), maximum height of stem blackening in white pine (*Pinus strobus* L.) (Beverly and Martell 2003), and maximum height of bole char in ponderosa pine (Regelbrugge and Conard 1993) have all been used as surrogate measurements for fire related cambium injury and have been shown to be important predictors in postfire mortality. Other studies (e.g. Ryan et al. 1988) have directly sampled the cambium to determine damage; however this measurement, due to time constraints in postfire management decisions, is not a practical nor is it a time efficient measurement of stem damage. While not greatly influencing mortality of larger trees, CHAR did contribute to mortality in trees less than 40 cm DBH (Fig. 2.3). As trees exceeded 40 cm DBH, even CHAR measurements of 75 to 100% contributed only a maximum of a ~20% increase in the probability of mortality. Without crown scorch, therefore, potential girdling as measured by CHAR does not significantly contribute to tree death and survival; however, in combination with crown scorch, increased CHAR significantly decreased postfire survival especially in trees less than 40 cm DBH. While large diameter trees (>40 cm) can be found throughout the Black Hills, they are rare on the landscape. The average size of a tree in the Black Hills is significantly smaller than 40 cm with the majority of the total live tree volume occurring in trees between ~23 and 28 cm DBH (Deblander 2002). Given the data presented from this study, CHAR, therefore, should be expected to significantly influence postfire mortality of the majority of ponderosa pine in the Black Hills. The importance of stem damage as a predictor of mortality in small diameter ponderosa pine trees, in particular, has been demonstrated through experimental manipulation of bark defenses and fuel loading around individual trees by van Mantgem and Schwartz (2004) in central California. Van Mantgem and Schwartz (2004) suggest that, similar to mortality in the absence of fire, postfire mortality is an additive effect of damage to different tree structures and organs and(or) interruption of important physiological functions such as cambial and crown damage which impact photosynthesis and water/nutrient transport.

In model 8, which predicted mortality as a function of the BARK, crown, and stem damage, BARK significantly influenced mortality (Table 2.1; Fig. 2.3). All models using BARK were statistically better models than those using DBH based on ROC values. The increase in model significance implies that resistance to cambium damage is more accurately measured by BARK rather than DBH. Studies using bark thickness as a function of DBH to predict mortality are not often based off of actual field measurements of bark thickness on burned trees; rather predictions of bark thickness are often based on species-specific DBH and BARK relationships (Ryan and Reinhardt 1988) or off-site, unburned trees (Harmon 1984). This method of determining BARK, however, does not take into consideration variation in bark thickness due factors such as age-related differences (van Mantgem and Schwartz 2003, Regelbrugge and Conard 1993). We took direct measurements of BARK and found that mortality was more responsive to small changes in BARK rather than DBH with only slight increases in BARK resulting in a greatly reduced predicted probability of mortality even in combination with high levels of PSCOR and CHAR (Fig. 2.3). For example, trees with BARK of 1 cm, were able to withstand 70% PSCOR and 75% CHAR before mortality occurred whereas trees with BARK of 2 cm were able to survive following both 100% PSCOR and CHAR.

Management implications

The use of bark thickness instead of DBH produced a model with better statistical properties; however the resultant increase in the overall estimated model accuracy was only 1% which was the direct result of accurately predicting the status of live trees versus actual mortality within the test dataset. Bark thickness is a time consuming measurement to take especially in the context of postfire salvage marking operations. The relatively small increase in the accuracy of discriminating between live and dead trees, therefore, does not warrant taking BARK measurements or including BARK as a variable in marking guidelines.

We have shown that model 4, which uses DBH in conjunction with PSCOR and CHAR, can predict 5-year postfire mortality of ponderosa pine in the Black Hills with an overall estimated accuracy of 78%. This model did not detect observed mortality within the test dataset as reliably as it predicted survival; however misclassifications of tree status may be due factors such as extreme measurements within the dataset or long-term delayed mortality. Many of the trees that were misclassified in the validation run possessed high levels of PSCOR in combination with low levels of CHAR. In addition, many of the trees that were misclassified as live by the end of the five year period did not die until the third or fourth year postfire suggesting that our explanatory variables may be less sensitive to long-term causes of mortality. More detailed measurements of crown damage such as percent of crown volume scorched in lieu of PSCOR may account for the misclassification of tree status due to extreme values associated with high PSCOR and low CHAR. Similarly, additional explanatory variables such as ground char severity or other variables that could potentially explain root damage could aid in the long-term predictive ability of the model (Swezy and Agee 1991). The addition of explanatory variables may produce a model with better statistical properties and improve the predictive power of the model. However, additional variables associated with more time-consuming measurements in the field could result in the model being more difficult to implement during postfire management planning processes with only a potentially slight improvement in the ability to discriminate between the future status of fire-affected trees.

The goal of model calibration was to produce the simplest yet most accurate postfire mortality model for ponderosa pine in the Black Hills given easily and efficiently measured morphological and first-order fire effects variables. We found that 3-variable equations (model 4 and model 8) resulted in significant improvements in predictive power over 2-variable mortality equations (models 3, 6, and 7) suggesting the stem damage as measured by CHAR has an important role in determining whether a tree lives or dies especially in trees of smaller size. The incorporation of stem damage into postfire mortality models increases a land manager's ability to discriminate between those trees that will die and those trees that will survive throughout the immediate years following fire. This increased predictive power will aid managers in making more science-based postfire management decisions and designing more ecologically sound postfire management operations. The assurance that postfire management operations are implemented based on the best available science and most recent models including measures of tree size, crown damage, and stem damage helps to ensure that salvage operations remove only trees with a high probability of dying postfire while leaving those trees predicted to survive. Minimizing the removal of postfire survivors would increase the retention of live trees and minimize the ecological impacts that have been proposed to be associated with salvage operations (e.g. Donato et al. 2006) and assures natural postfire recovery processes (i.e. postfire regeneration) occur while still allowing for the recuperation of resources following large-scale wildfires.

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List of Tables

List of Figures

Table 2.1. Five-year postfire mortality models for ponderosa pine following the Jasper fire in the Black Hills, SD. β_0 through β_4 are model coefficients corresponding to the intercept, DBH (models 1-4) or BARK (models 5-8), PSCOR, CHAR, and DBH*PSCOR (95% log likelihood asymptotic confidence intervals). -2LL represents the -2 Log Likelihood value, H-L is the Hosmer-Lemeshow goodness of fit test [$P(\chi) > \chi^2$], and ROC is the value associated with the receiver operations characteristic (ROC) curve analysis.

Model	β_0	β_1	β_2	β_3	B_4	-2LL	H-L	ROC
				Models using DBH (n=722)				
1. DBH	1.659† (1.209, 2.123)	-0.094† (-0.116, -0.074)				899.0	0.076	0.70
2. DBH, PSCOR, DBH*PSCOR	1.104* (0.044, 2.185)	-0.156† (-0.213, -0.103)	0.013 (-0.002, 0.027)		0.001* (0.0001-0.0015)	757.9	0.072	0.82
3. DBH, CHAR	1.223† (0.745, 1.712)	-0.092† (-0.115, -0.070)		0.027† (0.019, 0.034)		835.5	0.633	0.75
4. DBH, PSCOR, CHAR	-0.237 (-0.825, 0.350)	-0.098† (-0.123, -0.074)	0.027† (0.021, 0.032)	0.022† (0.015, 0.030)		724.0	0.558	0.83
				Models using BARK (n=721)				
5. BARK	2.556† (2.092,3.046)	-2.389† (-2.791,-2.012)				772.0	0.036*	0.80
6. BARK, PSCOR	0.915† (0.317,1.522)	-2.153† (-2.571,-1.759)	0.022† (0.017,0.027)			699.2	0.599	0.84
7. BARK, CHAR	2.059† (1.574,2.567)	-2.256† (-2.664,-1.873)		0.022† (0.015,0.030)		732.8	0.341	0.82
8. BARK, PSCOR, CHAR	0.538 (-0.086,1.169)	-2.038† (-2.460,-1.640)	0.021† (0.016,0.026)	0.019† (0.012,0.027)		671.5	0.567	0.86

NOTE: Regression coefficients and H-L tests are significant at: *α=0.05 and †α=0.01.

Table 2.2. Classification table displaying the results of the model validation for postfire mortality as a function of (a) model 4 which had an overall accuracy of 78.4 % and (b) model 8 which had an overall accuracy of 79.3%. The sum of the percentages from those trees observed dead and predicted dead and those trees observed live and predicted live results in the overall percentage of trees whose status was accurately predicted by each of the models.

(a)	Observed Dead	Observed Live	Total	(b)	Observed Dead	Observed Live	Total
Predicted dead	33.2% (*n*=80)	8.3% (*n*=20)	41.5% (*n*=100)	**Predicted dead**	33.2% (*n*=80)	7.5% (*n*=18)	40.7% (*n*=98)
Predicted live	13.3% (*n*=32)	45.2% (*n*=109)	58.4% (*n*=141)	**Predicted live**	13.3% (*n*=32)	46.1% (*n*=111)	59.4% (*n*=143)
Total	46.5% (*n*=112)	53.5% (*n*=129)	100% (*n*=241)	**Total**	46.5% (*n*=112)	53.6% (*n*=129)	100% (*n*=241)

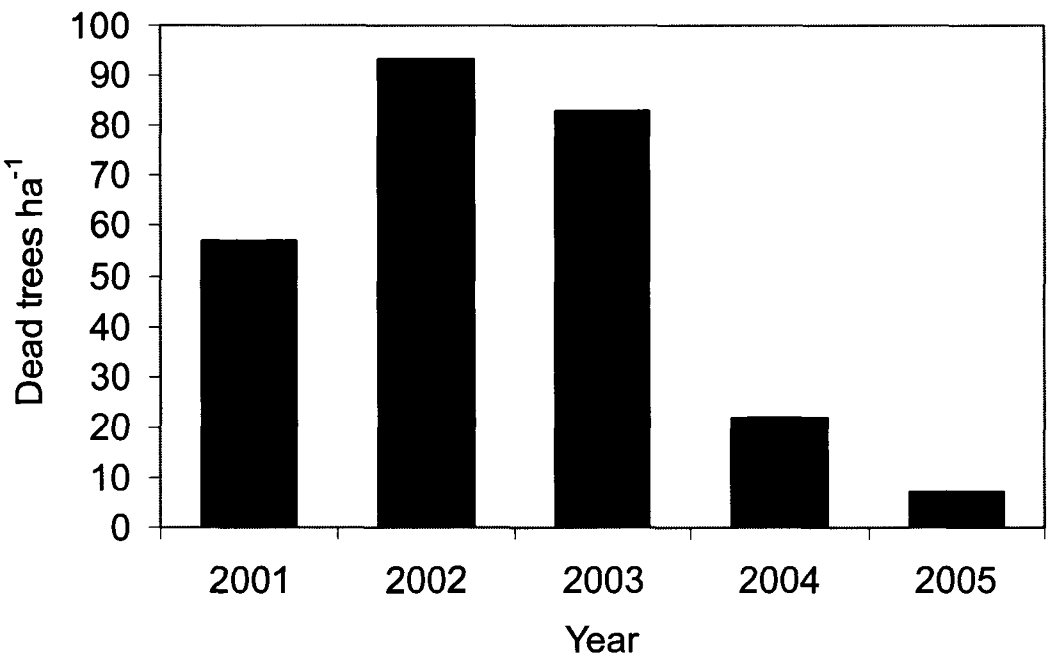

Fig. 2.1. Ponderosa pine mortality (ha^{-1}) within an individual year 1, 2, 3, 4, and 5 years postfire.

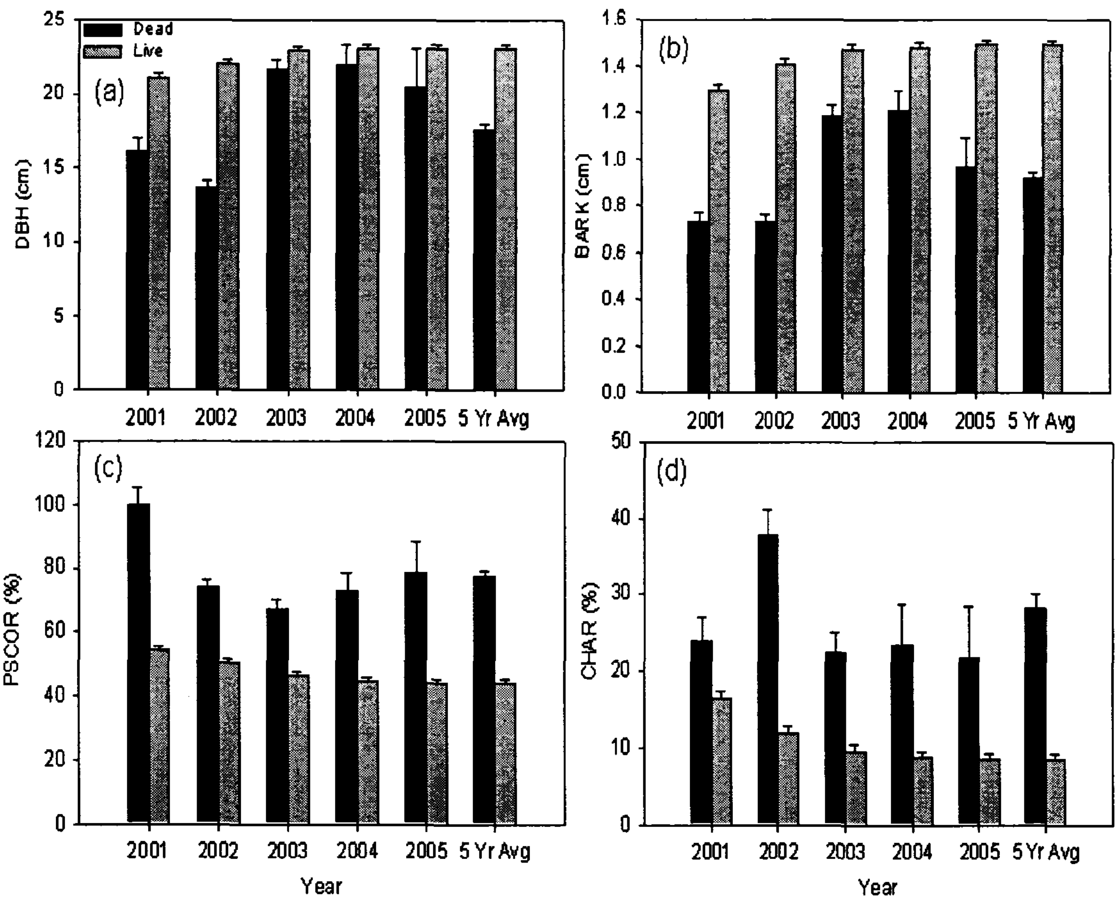

Fig. 2.2. Average (a) DBH (cm), (b) BARK (cm), PSCOR, and (d) CHAR for live and dead trees within a given year 1, 2, 3, 4, and 5 years postfire as well as the 5-year cumulative average. Error bars represent ±1 SE.

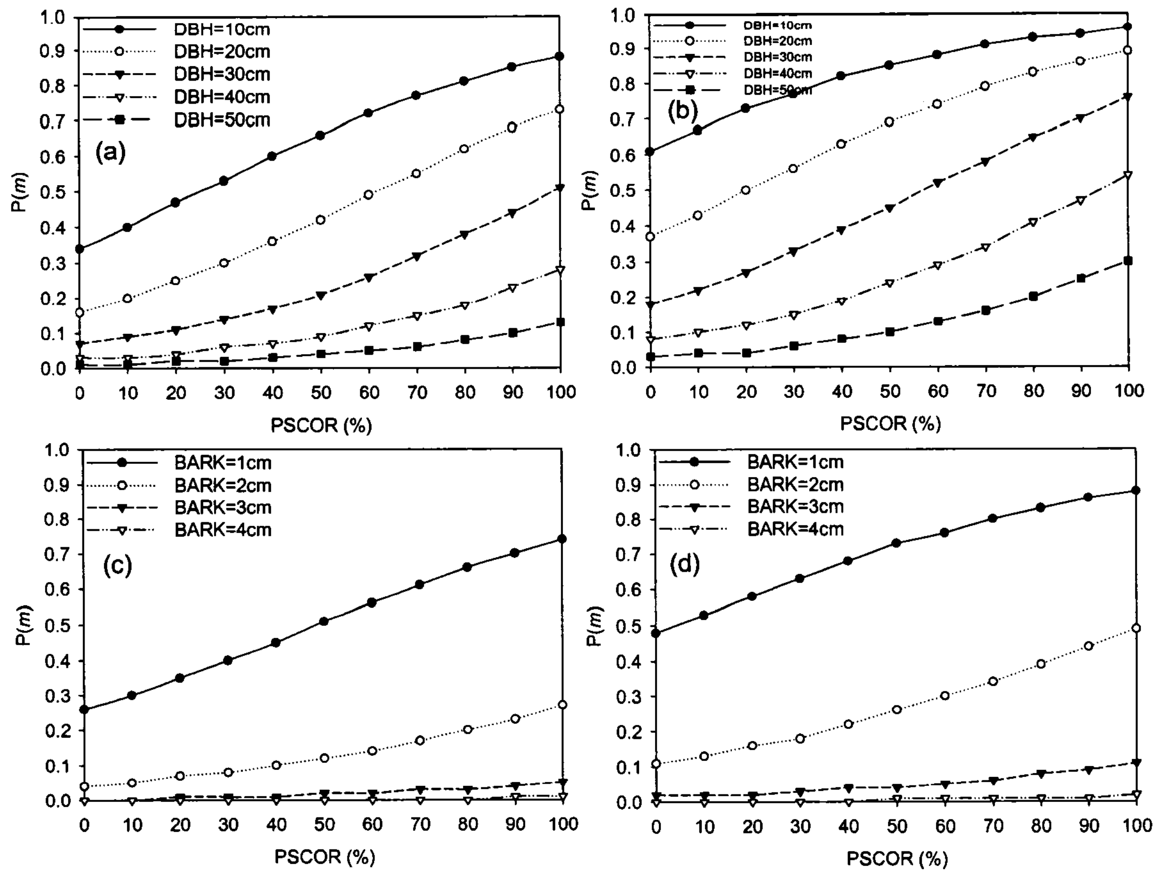

Fig. 2.3. Probability of mortality [P(*m*)] of ponderosa pine as predicted by (a) model 4, CHAR=25%, (b) model 4, CHAR=75%, (c) model 8, CHAR=25%, and (d) model 8, CHAR=75% 5 years postfire.

III. TEMPORAL CHANGES IN FOREST STRUCTURE FOLLOWING A LARGE-SCALE, MIXED-SEVERITY WILDFIRE IN PONDEROSA PINE FORESTS OF THE BLACK HILLS, USA.

ABSTRACT

We examined the effects of fire severity on the recovery of the forest overstory and forest floor throughout the 5 years following a large mixed-severity wildfire in ponderosa pine (*Pinus ponderosa* Laws.) forests of the Black Hills, SD, USA. Fire behavior varied across the landscape and was characterized as low-intensity surface fire, moderate-intensity surface fire with torching, and high-intensity active crown fire. Variations in fire behavior resulted in spatially variable patterns of fire severity across the landscape ranging from low severity fire effects to complete consumption of aboveground vegetation and organic matter. Low severity fire resulted in little change in overstory structure but had a significant impact on the forest floor. Tree mortality was largely limited to trees <20 cm dbh resulting in only a 5% decrease in basal area (BA), but a reduction in tree density of ~30%. Low severity fire consumed both fine woody debris (FWD) and coarse woody debris (CWD) and, due to limited tree mortality which limited the amount of dead fuel that could accumulate postfire, remained 60% less than unburned stands. Moderate severity fire caused tree mortality throughout the range of diameter classes (5 – 50 cm) resulting in a ~50% reduction in BA and a lifting of the forest canopy. Both FWD and CWD were reduced immediately postfire, but due to the

fall of fire-killed snags between 3 and 4 years postfire, quickly recovered to levels observed in unburned stands. In stands that experienced high severity fire, no living overstory remained. This lack of overstory seed trees resulted in a lack of ponderosa pine seed source which will make the rapid recovery to a closed-canopied forest unlikely. Initial reductions in FWD and CWD were diminished at the end of 5 years when FWD recovered to ~14 Mg/ha and CWD increased to 30 Mg/ha, 75% greater than CWD in unburned stands due to snag-fall of fire-killed trees. Differential effects of fire severity on the overstory and forest floor interact with management objectives to influence the need for postfire rehabilitation. Given the heterogeneity of fire effects, appropriate responses to mixed-severity wildfires include stand-level mitigation measures ranging from no action in areas of low severity fire to more intense actions such as planting in high severity areas.

INTRODUCTION

Understanding the relationship between fire behavior, direct fire effects, and postfire recovery in ponderosa pine forests from the effects of wildfire is critical in assessing the need for postfire rehabilitation. Direct fire effects include injury and death of individual trees, reduction of canopy cover and consumption of litter, duff and woody debris. The degree of departure of the postfire forest structure from that of prefire structure is directly related to fire behavior and the severity of the resultant fire effects. Fire behavior and fire effects in ponderosa pine (*Pinus ponderosa* Laws.) forests can vary within a single fire event along a continuum from low-severity surface fire (e.g. <25% overstory tree mortality) to high-severity active crown fire (e.g. ~100% overstory tree mortality) (Fule´et al. 2003, Lentile 2005). Due to variability in fire behavior, mixed-severity fires produce a spatially complex mosaic of fire effects across the landscape, where severity depends upon fine-scale changes in topography and stand structure (Lentile et al. 2006). Patches sizes of low, moderate, and high severity following recent mixed-severity fires can vary greatly ranging anywhere from <10 ha (Lentile et al. 2005) in ponderosa pine forests of the Black Hills to >3500 ha in mixed-conifer forests of the Colorado Front Range (Graham 2003). The end result of this spatial variability in burn pattern is a heterogeneous landscape with distinct patches of vegetation experiencing varying degrees of fire effects within close proximity to one another (Taylor and Skinner 1998, Fule´et al. 2003, Odion et al. 2004, Lentile 2005). Information regarding postfire stand dynamics and ecological succession following mixed-severity fires in ponderosa pine forests is not as well-developed as in other forest types due, in part, to the spatial variability in fire behavior that can occur within these ecosystems. In this paper, we evaluate the immediate effects of a large, mixed severity fire on forest structure in ponderosa pine forests of the Black Hills, South Dakota and compare the processes of forest recovery in areas burned under different severities.

Changes in stand structure following wildfire are the result of postfire tree mortality and subsequent changes in the density and size distribution of overstory trees (Stephens and Moghaddas 2005). For ponderosa pine, immediate and delayed tree mortality increases with increasing crown damage and (or) stem damage, but decreases with increasing tree size for a given amount of damage (Stephens and Finney 2002, McHugh and Kolb 2003, Hely´ et al. 2003, Keyser et al. 2006). Low severity fires result in less severe fire effects on prefire vegetation (e.g. crown damage), therefore, tree mortality is minimal and restricted to small diameter trees, often resulting in less than 20% of the prefire stand basal area (BA) being killed (Agee 1993, Hessburg et al. 2005). In contrast, tree mortality in areas of moderate and high severity fire is significantly greater. Here, the increased severity of fire effects (e.g. increased crown and stem damage) results in mortality of larger trees resulting in a 20-70% reduction in prefire stand BA (Hessburg et al. 2005). Regardless of tree size, high severity fire effects such as the complete loss of crown biomass and (or) high instances of cambial death results in ~100% overstory tree mortality (DeBano 1998). Structural changes may not be immediately apparent following fire. A significant proportion of postfire mortality, especially of large trees, may not occur until 3 to 4 years post-fire (Ryan et al. 1988, Agee 2003, Keyser et al. 2006).

Spatially variable patterns of fire severity, patch size, and overstory mortality (Agee 1993) influence postfire seed availability, regeneration, and recruitment of forest tree species (Greene et al. 1999, Greene et al. 2005). Postfire seed availability and regeneration determine future species composition, tree size, and age structure (Green et al. 1999, Miyanishi and Johnson 2002, Greene et al. 2005). Conditions most conducive to the germination and establishment of ponderosa pine include open growing conditions as well as areas of exposed mineral soil (Chappell and Agee 1996, Bailey and Covington 2002, Charron and Greene 2002, Bonnet et al. 2005). Fire promotes these conditions through the selective removal of overstory trees which increases light availability (Bond-Lamberty et al. 2002, Hale 2003, Comeau 2006) and improves seedbed quality through the reduction of both the litter and duff organic layers (Mackenzie et al. 2004, Knapp et al. 2005, Kasischke and Johnstone 2005). Initial changes in the depth of the organic layer are the result of fuel consumption where greater fire intensity and residence time result in a greater reduction in forest floor depth and mass (Brown et al. 1991, Little et al. 2002, Miyanishi and Johnson 2002, Kasischke and Johnstone 2005, Knapp et al. 2005). Bonnett et al. (2005) suggest that while the amount of ponderosa pine seedling germination is increased in areas containing exposed mineral soil, the harsh microenvironment (e.g. extreme temperature fluctuations and soil moisture deficits) of bare mineral soil may limit survival and recruitment. The authors contend that abscised scorched needles enhance germination and establishment by ameliorating temperature extremes and increasing soil moisture retention. Consequently, germination and establishment following mixed-severity fire should be greatest in areas of high needle scorch, high ground char, and moderate overstory mortality.

Coarse woody debris [woody biomass >7.6 cm diameter (CWD)] fills an important niche in forested ecosystems, providing habitat for vertebrate species as well as an energy and nutrient substrate for invertebrate, fungal, and microbial species (Harmon et al. 1986). The nutrients and energy released during decomposition of woody organic matter contribute to the maintenance of long-term site productivity. For these reasons, land managers must often maintain minimum amounts of woody biomass within a given forest stand. Optimal amounts of CWD for maintaining productivity in ponderosa pine systems throughout the Rocky Mountain region have been suggested by Graham et al. (1994) to vary between ~11 and 30 Mg/ha.

Fire may remove and (or) add CWD and fine woody debris [woody biomass <7.6 cm diameter (FWD)] to the forest floor. Both FWD and CWD factor into potential fire behavior, which is often a concern following large wildfires due to the potential for a reburn. Initial reductions in FWD and CWD are often short-lived as portions of, or entire fire-killed trees, fall to the ground quickly contributing to a site's fuel loading (Passovoy and Fule′ 2006). Chambers and Mast (2005) report that 7 years following severe crown fire in northern Arizona, 41% of all fire-killed ponderosa pine trees had been broken or uprooted. In comparison, the authors reported only a 26% snag-fall rate in a comparable unburned plot, providing additional evidence that fire-killed snags fall more rapidly than unburned snags. Given that tree mortality increases with increasing fire behavior and severity (Ryan et al. 1988, Keyser et al. 2006, Thies et al. 2006), the potential for significant fuel build-up should, therefore, also increase with increased fire severity.

The removal of organic matter (e.g. litter, duff, and woody biomass) impacts nutrient availability following fire. While postfire (1-5 year) losses of total organic nitrogen are significant (Caldwell et al. 2002, Murphey et al. 2006), plant available nitrogen (PAN) often increases immediately following fire (Deluca and Zouhar 2000, Prieto-Fern′andez et al. 2004). Available nitrogen in the form of ammonium (NH_4^+) is produced during a fire through the decomposition and pyrolysis of organic nitrogen compounds (St. John and Rundel 1976, Mroz et al. 1980) whereas nitrate (NO_3^-) is produced via nitrification of NH_4^+ (Convington and Sackett 1986, Covington and Sackett 1992). The impacts of mixed-severity wildfire on postfire nitrogen availability are not fully understood as most studies that examined nutrient cycling were carried out in controlled prescribed fires, which were designed to reduce fuel loadings (e.g. Covington and Sackett 1992). However, following fire PAN is proportional to the amount of organic matter consumed (White 1986), therefore increased fire severity and fuel consumption should increase PAN (Smithwick et al. 2005). The increase in PAN, while short-lived, can have dramatic effects on the re-establishment of understory vegetation as well as postfire seedling germination and growth (Covington and Sackett 1992).

In this study, we measured direct fire effects and monitor 5 years of postfire change in vegetation, forest floor, and soil to study the impact of a mixed severity wildfire in ponderosa pine dominated forests of the Black Hills. Compared to surface and crown fire dominated fire regimes, mixed-severity fires and their effects on numerous ecosystem components are not well understood or documented. Specifically, we evaluate the short-term impact of fire behavior and fire severity on postfire overstory structure, forest floor structure, surface woody fuel loadings, postfire regeneration, and nitrogen availability to provide information regarding the long-term changes in the postfire structure of forest stands affected by different fire severity in the Black Hills. The results and interpretation of this study will provide land managers with scientifically-based information regarding the short- and long-term changes in forest structure following mixed-severity wildfire.

METHODS

Study area

The study was located within the Jasper fire perimeter in the Black Hills National Forest, South Dakota, USA (latitudes between 43° 42' and 43° 57' and longitudes between 103° 46' and 104° 1'). The Black Hills are an isolated, forested uplift that rise ~900-1200 m above the surrounding Great Plains in southwestern South Dakota and northeastern Wyoming (Froiland 1990, Hoffman and Alexander 1987). Dominant soils types are similar throughout the area and are mainly loamy-skeletal, frigid Inceptic or

Glossic Hapludalfs, loamy-skeletal, frigid Typic Haplustalfs, or loamy-skeletal, frigid Lithic Haplustolls (Bryce et al. 1998, Shepperd and Battaglia 2002). The climate is a continental with cold winters and mild, moist summers (Johnson 1949). Mean maximum and minimum daily temperatures range from -3.3 and 13.2 and yearly precipitations averages ~47 cm with 65-75% occurring between the months of April and October (Hoffman and Alexander 1987, Froiland 1990, Shepperd and Battaglia 2002).

On August 24, 2000, the Jasper fire was ignited near the town of Custer, SD during a period of record low fuel moisture conditions and extremely unstable atmospheric conditions, leading to strong wind gusts and a maximum rate of spread of 16 ha/minute (Lentile et al. 2006). The fire was contained on September 8, 2000 after burning ~34,000 ha or ~7% of the Black Hills National Forest (Shepperd and Battaglia 2002, USDA 2000). The Jasper fire was a mixed-severity fire producing a combination of surface fire (low fire behavior), surface fire with torching (moderate fire behavior), and active crown fire (extreme fire behavior). The fire burned through predominantly ponderosa pine and left behind a mosaic of low, moderate, and high severity fire effects across the landscape (Lentile et al. 2005).

Experimental design

Following the fire and in collaboration with Black Hills National Forest staff, we identified 3 – 800 ha forest units in which no postfire silvicultural activities (e.g. salvage harvesting) would occur. These three units had each experienced a combination of low, moderate, and high fire behavior. In June 2001, we randomly established 36 – 0.3 ha permanent study sites in burned and unburned ponderosa pine stands within and immediately outside the Jasper fire perimeter. Sites were established in a complete block design with forest units serving as the block and fire severity serving as the treatment. Each block contained 3 replicates of each fire severity class. Twenty seven of the 36 sites were located in ponderosa pine stands that exhibited evidence of having burned under different types of fire behavior. Sites were established within treatments or fire severity classes which we assigned based on the indicators of fire behavior reported by Lentile et al. (2005) (Table 3.1). Within the burned stands, 9 sites were located in areas exhibiting evidence of surface fire behavior (treatment = low severity), 9 sites were located in stands exhibiting evidence of moderate fire behavior consisting of surface fire with individual tree torching (treatment = moderate severity), and 9 sites were located in areas exhibiting evidence of active, stand-replacing crown fire (treatment = high severity). The remaining 9 sites were located in adjacent unburned pine stands and served as our control sites (treatment = unburned).

We recognize that using adjacent unburned sites as a basis for comparing fire effects on the forest floor and soil nitrogen requires that we assume no differences existed between the burned and unburned sites prior to the fire. This assumption, however, seems reasonable given the similarity in stand structure among burned and unburned stands. Numerous studies (e.g. Fule′ et al. 2004) have used adjacent unburned stands as a proxy for prefire controls for studying fire effects on existing vegetation.

Overstory measurements

Each of the 36 study sites contained of 3 – 0.03 ha overstory plots located at bearings of 0°, 135°, and 225° 20 m from site center. In early June 2001, prior to the fall of scorched needles and the onset of postfire tree growth, we tagged every tree ≥1.4 m in height, recorded species, and assessed tree mortality taking care to note any tree that was dead prior to the fire. Trees that were originally located within the overstory plots but had broken off or fallen between the time of the fire and the onset of measurements were tagged and included in the study. Unless labeled as a prefire dead tree, all dead trees were considered to have been alive prior to the fire. We measured tree diameter (cm) taken at 1.4 m above the soil surface (dbh), tree height (m), and the prefire height to the base of the live crown (HLC; m). All height measurements were measured using an Impluse® laser hypsometer (Laser Technology, Inc., Centennial, CO). Height to live crown was identified from the position of scorched needles in the case where no foliage consumption occurred and fine branch structure in the case where consumption of needles occurred and measured at the point of branch-bole attachment of the lowest prefire live whorl (Keyser et al. 2006).

On each tagged tree, we assessed the severity of direct fire effects by measuring crown and stem damage. Crown injury was measured on individual trees and included maximum height of needle scorch and consumption. Scorch height was measured as the maximum height on the crown where necrotic foliage occurred. Scorched needles were brown or orange in color and had not been ignited by fire. Consumption height was measured as the maximum height where foliage had been ignited and directly consumed by the fire. Stem damage, which served as a proxy for cambial injury, was measured as the percentage of the bole circumference charred below a height of 30 cm. Charred bark was metallic black in color and was eroded to the point the bark no longer contained grooves or furrows (Lentile 2004). We revisited study sites and assessed tree mortality annually between 2002 and 2005. In 2005, we re-measured dbh, tree height, and HLC on all residual live trees.

We measured above- and below-canopy photosynthetically active radiation (PAR), measured in $\mu moles \cdot m^{-2} \cdot sec^{-1}$, annually between 2001 and 2005 using a Sunfleck ceptometer (Decagon Devices, Inc., Pullman, WA) in 2001-2004 and an AccuPAR LP-80 (Decagon Devices, Inc., Pullman, WA) in 2005. Light samples, measured between the hours of 1000 and 1500 MST between June and August, were taken in each cardinal direction at 10 points in each overstory plot and averaged for each site. Above-canopy PAR measurements were taken in clear, unobstructed forest openings every 15 minutes and averaged for each site. Percent canopy light transmittance (CLT) for each site was calculated as (below-canopy PAR/open canopy PAR)*100. The 2002 PAR dataset was incomplete and therefore not included in the analysis.

Forest floor measurements

We monitored initial fire effects and postfire forest floor recovery at each site by measuring litter and duff depth and surface woody fuel biomass. We measured annual litter and duff depth every 2 m along a 60 m transect that ran 30 m east and 30 m west of each site center, and a yearly site averaged was calculated. In 2001, we estimated the proportion of the forest floor at each point along the transect with unburned ground, as well as low, moderate, and high severity ground effects (Ryan and Noste 1985). Using bulk densities specific for Black Hills ponderosa pine litter (60.7 kg/m^3) and duff (102.6 kg/m^3) developed by Battaglia (2007), we converted litter and duff depths to estimates of forest floor mass (Mg/ha). We estimated both FWD (woody material <7.62 cm; Mg/ha) and CWD (woody material >7.62 cm; Mg/ha) at each site using the planar intersect method described by Brown et al. (1982). Fine fuels were measured along 10 m of the

60 m transect and coarse fuels were measured along the entire transect.

Postfire tree regeneration

We measured ponderosa pine regeneration annually from 2001 to 2005 using 50 - 1 m^2 regeneration plots randomly located throughout each 0.3 ha site. Within each regeneration plot we counted the number of seedlings <1.4 m in height and determined seedling age by back-counting the bud scale scars from current year growth. Only seedlings that germinated postfire were counted. Seedling age was not determined in 2001; therefore we did not include regeneration data from that year in the analysis as we were interested in exploring how postfire regeneration varies in response to fire severity.

Soil nitrogen

We used ion-exchange resin bags (Binkley and Matson 1983) to index postfire total PAN ($NH_4^+ + NO_3^-$). Four resin bags were placed in each overstory tree plot in all burned and unburned sites in May of 2001. In May of 2002, resin bags were collected and replaced with new resin bags. After collection, resin bags were immediately air dried. Resins were extracted with 100 mL of 2*M* KCL and analyzed for ammonium and nitrate on an Alpkem Flow Solution IV Automated wet chemistry system (O.I. Analytical, College Station TX). This process was repeated annually through 2005.

Statistical Analysis

Prefire stand density, BA, average stand diameter (ASD), and HLC were analyzed as a one-way analysis of variance (ANOVA) to determine if prefire stand structure varied among fire severities. Postfire measurements and yearly changes in overstory attributes, CLT, postfire tree regeneration, litter and duff mass, FWD and CWD, and PAN were analyzed as a repeated measures ANOVA to determine the effects of fire severity (unburned, low, moderate, and high) and time (1-5 years postfire) on postfire overstory and forest floor development (SAS Institute 2005). Covariance structures for the repeated measures were modeled as either a first-order autoregressive model or a first-order autoregressive model with heterogeneous variances with site included as a random variable. Separate ANOVAs were performed to test the impact of fire severity each year because the repeated measures analysis indicated significant severity x year interactions for almost all response variables. Following significant F-tests, pairwise multiple comparisons among treatments were performed using LSD (Steel et al. 1997). Response variables were $\log_e + 1$ transformed, square root transformed, or arc sin-square root transformed when necessary to approximate normality and homoscedasticity (Steel et al. 1997). The means and standard errors we report are from the raw, untransformed data. Analyses were significant at $\alpha = 0.05$.

RESULTS

Prefire forest structure and direct fire effects

Prior to the Jasper fire, our research sites were well-stocked, pure, second growth even-aged ponderosa pine stands. Stand density averaged ~670 stems/ha and BA was 24 m^2/ha (Table 3.2). Stands were moderately sized with an ASD of ~22 cm. Mean height and HLC were ~13 and 5.5 m. The relatively low prefire HLC reflects the abundance of small diameter trees within these stands. Prefire density, BA, ASD, and HLC did not differ among fire severities ($P > 0.17$). Therefore, subsequent changes in postfire forest structure can be attributed to direct fire effects and fire-caused damage to the existing prefire vegetation.

Fire behavior during the Jasper fire varied between low-intensity surface fire and high-intensity crown fire, evidenced by variation in direct fire effects throughout the burned area. Vegetation that burned under low-intensity surface fire had significantly less fire-caused damage than areas that burned under progressively greater fire intensity and more extreme fire behavior. The maximum height of crown scorch, which is related to flame length and fire intensity (Finney and Martin 1993, van Wagner 1973), ranged from ~8 m in low severity sites to ~14 m in high severity sites. Trees in low severity sites had minimal crown damage; however total crown damage significantly increased with increases in fire severity (Fig 3.1). Basal char was similar between low and moderate severity sites and averaged ~9 ± 4% and 19 ± 6%. This suggests that fire residence times and (or) the degree of smoldering combustion that occurred around the basal portions of individual trees was similar between these two fire severities. The amount of basal char recorded in high severity sites was significantly greater than in both low and moderate severity sites averaging 55 ± 8% providing further evidence of increased fire intensity within these sites.

Tree mortality

Initial tree mortality was directly related to fire severity with fire-caused mortality occurring throughout the 5 years of this study. Complete overstory mortality occurred immediately following the fire in areas that burned under high severity. Consequently, we limit comparisons of postfire forest structure through time and among fire severities to unburned sites and those sites that burned under low and moderate fire severity. Small tree density (trees ≥5 cm and <15 cm dbh) varied among fire severities within individual years ($F = 3.0$, df = 8, 95.6, $P = 0.0051$) (Fig. 3.2a). At the end of 5 years, moderate severity fire resulted in a 100% reduction in small tree density. In comparison, at the end of 5 years, small tree density in low severity sites had been reduced by 64% from prefire levels.

Similar patterns of mortality were observed in regards to the effects of fire on large tree density (trees ≥15 cm dbh) in low and moderately burned sites. The response of large tree BA was dependent upon fire severity but varied within individual years (F = 17.2, df = 8, 96, $P < 0.0001$) (Fig. 3.2b). Basal area of trees ≥15 cm dbh in stands of moderate fire severity was reduced from 22 m^2/ha prior to the fire to just 13 m^2/ha by the 3rd year postfire. Mortality of large diameter trees slowed between 3 and 5 years postfire, during which time BA was further reduced by an additional 15%. Reductions in large tree BA were insignificant in low severity stands where large tree BA was reduced by only 5% at the end of 5 years.

Timing of mortality and the sizes of trees that died varied in stands impacted by low and moderate fire severity. One year postfire little to no mortality occurred in low severity sites (Fig. 3.3b). By 2 years postfire, 50% of small trees died and, for this first time since the fire, mortality occurred in the 20 cm size class. The greatest increase in mortality in low severity sites between 2 and 3 years postfire occurred in the 20 cm size class where an increase in mortality of 11% occurred and for the first time, mortality occurred in the 30 cm size class. Between 3 and 5 years postfire, only minor amounts of mortality occurred within the low severity sites with mortality limited to the three smallest size classes.

The timing and size of tree mortality in moderate severity sites differed substantially from the pattern observed in low severity sites (Fig. 3.3c). Immediately postfire, mortality in moderate severity sites included all size classes as opposed to low severity sites where mortality was confined to the smaller size classes. Sixty-nine percent of small trees died immediately and mortality of small trees reached ~100% 3 years postfire. Cumulative mortality in medium sized trees (20 and 30 cm size classes) increased from 13% immediately following the fire to 48% 3 years postfire. Similarly, mortality of large trees (40 and 50+ cm size classes) increased from 5% immediately postfire to 40% 3 years postfire. There was little additional mortality between 3 and 4 years postfire and mortality had all but ceased in these moderate severity sites by the 5th year postfire.

Stand structure

Tree mortality impacted overall stand structure; however, the degree of departure from prefire structure was dependent upon fire severity. The combined and accumulated mortality of small and mid-sized trees following low severity fire resulted in a significant reduction in overall stand density from that observed in unburned stands, however overall BA remained unchanged (Table 3.2). In moderately burned sites, significant mortality within all size classes resulted in a significant reduction in overall stand density as well as stand BA. The complete mortality of small diameter trees increased ASD by an average of 5 cm in moderate severity sites whereas enough small diameter trees remained in low severity sites that ASD remained similar to unburned stands. The HLC increased in moderate severity sites by an average ~3.5 m over that in comparable unburned stands while the relative abundance of small and mid-sized trees in low severity sites kept HLC similar to that in comparable unburned stands.

Canopy light transmittance increased with increased fire severity ($F = 70.1$, df = 3, 43.6, $P < 0.0001$). The lowest CLT was observed in unburned sites where minor levels of overstory mortality were recorded throughout the study period and where an average of only 36% of PAR reached the forest floor (Table 3.2). As fire-caused mortality occurred in burned stands over the 5 year measurement period, CLT increased and resulted in an average of 15, 32, and 49% more PAR in areas of low, moderate, and high severity than in unburned stands.

Forest floor

Litter mass varied in response to fire severity within individual years ($F = 13.4$, df = 12, 41.4, $P < 0.0001$). Compared to unburned sites, litter was initially reduced by 68% in low severity sites, 88% in moderate severity sites, and 92% in high severity sites (Table 3.3). Two years postfire, after the abscission of scorched needles, litter mass had increased to ~10 Mg/ha in both low and moderate severity sites but remained lower than in unburned sites. At the end of 5 years, litter mass in low severity sites was within 25% of that in unburned stands and litter mass in moderate severity sites was only 36% less than in comparable unburned sites. No increase in litter had occurred on high severity sites throughout the study.

Fire severity had a significant influence on the recovery of the duff layer, however the effect of fire severity varied within individual years ($F = 2.2$, df = 9, 51.6, $P < 0.0368$). Compared to an average duff mass of ~29 Mg/ha in unburned sites, duff was reduced by ~89, 95, and 98% in areas of low, moderate, and high severity two years postfire (Table 3.3). Little change in the duff layer occurred 5 years postfire at which time duff had only slightly increased in low and moderate severity sites. Similar to litter, there was no increase of duff mass at anytime during the 5 year study in high severity sites.

The response of FWD to fire severity varied within individual years ($F = 3.3$, df = 12, 52.9, $P = 0.0014$). One year postfire, FWD in low, moderate, and high severities was reduced by 64, 80, and 92%, respectively compared to unburned stands (Table 3.4). Between 2 and 5 years postfire, FWD steadily increased in both moderate and high severity sites such that at the end of 5 years, FWD had recovered to unburned levels. The reductions in FWD in low severity sites remained, however, with FWD 60% lower than in comparable unburned stands 5 years postfire.

Coarse woody debris was impacted by fire severity while recovery within severities varied within individual years ($F = 5.5$, df = 12, 67.3, $P < 0.0001$). The postfire recovery of CWD was similar to the recovery of FWD throughout the study period. Fuel reduction due to consumption during the fire caused a significant reduction in CWD in burned sites compared to CWD in the nearby unburned stands (Table 3.4). Compared to unburned sites, initial reductions in CWD in low, moderate, and high severity sites were 83, 86, and 81%, respectively. By the 3rd year postfire, little change in CWD had occurred in low and moderate severity sites, however CWD in high severity sites increased 330% over 2001 levels. Five years postfire, changes in CWD among the fire severities was even more dramatic. Coarse woody debris in low severity sites remained 61% lower than unburned sites; however, CWD in moderate severity sites had increased 890% over 2001 levels and were now equal to that in unburned sites. The largest 5 year increase in CWD occurred in high severity sites where CWD loads were 30 Mg/ha; almost twice the level observed in unburned stands.

Postfire tree regeneration

Postfire tree regeneration was variable throughout the 5 year study, however it was significantly influenced by the interaction between fire severity and year (F = 5.0, df = 9, 63, P < 0.0001). Little to no relationship was observed between fire severity and the amount and success of postfire tree regeneration among unburned, low, and moderate severity sites. Generally, unburned sites possessed equal or slightly greater amounts of tree regeneration than low and moderately burned sites (Fig. 3.4). As time progressed, postfire tree regeneration in high severity sites, however, was consistently lower than that observed in comparable unburned, low, and moderate severity sites.

Soil nitrogen

Total PAN is the sum of available NH_4^+ and NO_3^-. The influence of fire severity on PAN varied yearly (F = 7.1, df = 9, 55.1, P < 0.0001). One year postfire, the effect of severity on available nitrogen was highly significant with burned sites having greater nitrogen availability than unburned sites (Fig. 3.5). Between 1 and 5 years postfire, there was a progressive and steady decline of PAN within burned sites. At the end of 5 years, PAN had been reduced to unburned conditions in low and moderately burned sites; however PAN continued to be elevated in areas that experienced high severity fire.

DISCUSSION

Mixed severity regimes are complex, single event fires in which fire behavior varies along a continuum from surface fire to active crown fire and creates variable fire effects across the landscape (Agee 1993, Lentile et al. 2005, 2006). Individual mixed severity fires are characterized by the juxtaposition of variable fire behavior and consequent fire effects within a single fire perimeter (Fule' et al. 2003). These fire effects are commonly characterized as burn or fire severity and are measured by the magnitude of damage to vegetation and soil often classified into distinct categories: low, moderate, and high severity (Lentile et al. 2006). High severity fire crown fire is linked to intense surface fire behavior (van Wagner 1977) in which severe fire effects on vegetation and soils cause complete mortality of aboveground vegetation and consumption of almost all organic matter. In contrast, low severity fire, which is linked to surface fire behavior, may be non-lethal to forest vegetation, but may still have substantial impact on forest floor and soils. In this paper, moderate severity fire was linked to passive crown fire which contained elements of severe surface fire and the torching of individual trees resulting in moderate levels of mortality and substantial and immediate impacts on the forest floor. Severe fire effects that can all be associated with low, moderate, or high severity fire include high rates of duff consumption, fine root mortality, and cambial damage all of which can contribute to immediate and delayed tree mortality (Swezy and Agee 1991, Stephens and Finney 2002) and the accumulation of hazardous surface fuels (Agee 2003).

We asked specifically how fire effects differed in areas of different severities and how the differences affected the processes and rate of ecological recovery to prefire conditions with respect to key structural components of vegetation and forest floor. The Jasper fire burned as a single mixed severity wildfire that created a mosaic of burn severity and initial fire effects across a 34,000 ha landscape. While the majority of the landscape burned under high severity active crown fire, significant proportions also burned under moderate or low fire behavior (Table 3.1). These areas of different fire behavior created a complex spatial pattern of fire effects. The Jasper fire created 2,672 identifiable patches of differing fire severity with a mean patch size of ~12 ha (Lentile et al. 2005). Substantial differences in postfire structure and subsequent ecological recovery within this ponderosa pine forest resulted from differences in the severity of direct fire effects. Areas impacted by low fire severity experienced low levels of tree mortality that were limited to small diameter trees, but experienced significant impacts on the forest floor. Forest stands impacted by moderate fire severity experienced significant tree mortality throughout the range of size classes and had substantial effects on the forest floor. In contrast, areas impacted by high severity fire experienced complete tree mortality and nearly complete consumption of biomass throughout the forest floor.

Low severity

Tree mortality in areas of low severity surface fire was largely limited to smaller trees. While 65% of trees <15 cm dbh died following fire, only 5% of trees between 15 and 35 cm died and no mortality occurred in larger trees (Fig. 3.3b). These results are consistent with fire effects similar to those observed following managed prescribed fire performed under relatively conservative weather and fuel moisture conditions that produce low intensity fire with low severity fire effects on forest vegetation. For example, Thomas and Agee (1986) observed that ponderosa pine mortality following prescribed fire in Oregon was limited to trees <20 cm dbh in the 1st 2 years following fire with only minor mortality of trees >30 cm occurring during the 3rd and 4th years postfire. Given the minor amounts of mortality in merchantable sized trees, there is no justification for value recovery efforts, such as postfire salvage activities, in these stands.

Limited tree mortality resulted in a modest departure of stand structure between low severity and unburned stands at the end of the 5 year measurement period (Table 3.2). While total stand density was reduced, stand BA, ASD, and HLC were not different for low severity and unburned stands throughout the 5 years of postfire recovery. Fule′ et al. (2006) reports that while stand density significantly declined following prescribed fire aimed at ecological restoration in northern Arizona, stand BA remained unchanged. As a result, low severity fire did not likely impact forest growth (Sutherland et al. 1991) or reduce crown fire hazard due to the residual amount and structure of canopy fuels (Agee and Skinner 2005).

Surface fire behavior associated with low severity fire within these stands substantially altered the structure and composition of the forest floor when compared to unburned stands. Some changes were only temporary and quickly approached unburned conditions by the end of the 5 years, while other changes persisted and showed no evidence of significant recovery after 5 years. Changes in the structure of the forest floor following fire were dependent upon the physical characteristics of the fuel bed including the amount of available fuel (i.e. woody fuel loading as well as litter and duff mass), fuel continuity, and fuel moisture (DeBano et al. 1998). The 61% reduction in litter mass we observed in our low severity wildfire sites immediately postfire was similar to what Fule′ et al. (2002) observed following managed, prescribed fire in ponderosa pine forests of the Southwest. While litter mass in these low severity sites did not return to unburned levels, litter did recover to within 25% of that in unburned sites as scorched needles abscised and fell to the forest floor (Table 3.3).

Consumption of duff during the smoldering phase of the fire (DeBano et al. 1998) resulted in what will likely be a long-term reduction in duff mass within low severity sites (Table 3.3). The Jasper fire burned under extreme weather conditions and low fuel moistures (USDA 2000), resulting in high duff consumption (Robichaud and Miller 1999). Compared to unburned sites, low severity fire resulted in an 89% reduction in duff, which is considerably greater than the 70% observed by Fule′ et al. (2006) after an intense prescribed fire performed under low humidity and high winds in northern Arizona. Reduced duff can lower smoke production during future managed (e.g. prescribed) or wildfire events, but burning of duff can cause fine root mortality (Swezy and Agee 1991) and cambial damage of large diameter trees (Stephens and Finney 2002). Furthermore, high duff consumption may not be desirable because of its role in stabilizing soil (Wells et al. 1979) and maintaining long-term nutrient dynamics following fire (Covington and Sackett 1986). In our sites where duff consumption was high, recovery to prefire levels will take several additional years since duff is formed via the long-term decomposition of surface litter (Robichaud and Miller 1999). It should not, however, be limited by future litter inputs (Hall et al. 2006).

Consumption of surface fuel followed by litter inputs from damaged trees creates changing potential fire behavior over time in the postfire environment. Immediately postfire there was a 65 and 83% reduction in FWD and CWD (Table 3.4). While FWD and CWD increased over 5 years within the low severity sites, they remained ~60% less than in unburned stands. Again these results are consistent with effects of prescribed fire in ponderosa pine forest (Fule′ et al. 2006). After 5 years, the majority of fire-killed small diameter trees have fallen but there was little mortality in larger trees; therefore we do not expect large additions to surface fuels in the near future as a direct result of the Jasper fire.

Moderate severity

Similar to the low severity stands, the majority of tree mortality following moderate severity fire occurred during the initial 3 years following the Jasper fire. Unlike low severity stands, however, mortality was not concentrated in the small diameter trees. Of all trees between ≥5 and <15 cm dbh 95% were dead by 3 years postfire and ~100% were dead at the end of 5 years (Fig. 3.2a). Mortality of large diameter trees was observed immediately postfire and occurred in even the largest trees (Fig. 3.3c). The greatest increase in mortality of large trees (≥15 cm dbh) occurred between 2 and 3 years postfire when large tree BA dropped to 13 m^2/ha. At the end of 5 years, delayed mortality within the upper canopy stratum resulted in a 52% reduction in large tree BA throughout the moderate severity sites demonstrating the extensive canopy effect moderate severity fire had on these forest stands. In areas where timber production is of concern, postfire salvage operations designed with locally developed mortality models (e.g. Keyser et al. 2006) provide the best opportunity to capture the immediate and incipient mortality in these moderate severity sites.

Moderate severity fire significantly altered stand structure from unburned conditions 5 years postfire (Table 3.2). Unlike low severity fire, both stand density and BA were significantly reduced from unburned conditions. The thinning effect of fire resulted in an increase in ASD, and HLC. The removal of the smaller diameter ladder fuels significantly decreases vertical and horizontal continuity of the canopy fuel stratum and coupled with the dominance of the stand by larger, more fire-resistant trees (Keyser et al. 2006) substantially reduces the risk of active crown fire in future fire events (Agee and Skinner 2005). The open stand structure with fewer large surviving trees that resulted from moderate severity fire mimics more intense ecological restoration treatments designed to protect larger living trees from crown fire and reduce tree competition in Southwestern ponderosa pine forests (Fule' et al. 2002)

Patterns of litter and duff consumption and postfire development in moderate severity sites were similar to those observed in low severity sites (Table 3.3). Following an initial reduction of 88%, litter mass quickly increased to within 34% of that in unburned stands 2 years postfire as scorched and fire-killed needles were shed and accumulated on the forest floor and appeared to stabilize within ~30% of that in unburned stands at the end of 5 years. Passovoy and Fule′ (2006) observed an increase in litter depth over a 27 year chronosequence following severe (e.g. >50% mortality) wildfires in northern Arizona. Therefore, even with the >50% mortality that occurred within these sites, long-term litter inputs should not be expected to further decrease.

The immediate 94% reduction in duff mass in our moderate severity sites was comparable to the 93% reduction observed by Knapp et al. (2005) following fall prescribed burns in a northern California mixed-conifer forest (Table 3.3). Again, a long-term reduction in duff is a goal of fuels treatment projects, however through its impact on fine root mortality and cambial damage, likely contributed to the delayed mortality of large diameter trees observed within these sites (Stephens and Finney 2002, Swezy and Agee 1991).

The substantial mortality of both small and large trees within moderate severity sites resulted in the accumulation of surface woody fuel. During the Jasper fire, moderate severity fire consumed 80 and 86% of the FWD and CWD, respectively (Table 3.4). However after 5 years, ~50% of all fire-killed biomass contained in trees >10 cm dbh had transitioned completely or partially from the vertical to horizontal fuel bed causing FWD and CWD to recover to unburned levels. Continued rates of fuel accumulation within these sites will depend on snag fall rates of fire-killed trees. Passovoy and Fule′ (2006) report that snag fall rates of fire-killed ponderosa pine trees and fuel accumulation following wildfire in northern Arizona increases with time since fire up through the 9th year postfire. The authors report that within 3-4 years, 22% of the snag population had fallen or broken while 78% had fallen or broken within 8-9 years-postfire. Provided snags continue to fall through the 9th or 10th year postfire (Harrington 1996), both FWD and CWD could exceed levels in unburned stands and the current limits recommended for managing both the ecological benefits and fire hazard associated with CWD (Brown et al. 2003).

High severity

Areas that burned under high severity active crown fire during the Jasper fire experienced the most dramatic and significant changes in terms of both overstory and forest floor structure. The extreme fire behavior and associated fire effects in these sites were severe enough to cause ~100% crown damage which, regardless of size, resulted in immediate and complete tree mortality.

The immediate impact high fire severity had on the forest floor remained throughout the 5 years following the fire (Table 3.3). Litter, which was initially reduced by 92%, was still only 7% of that observed in unburned stands 5 years postfire. The lack of litter accumulation in areas of high severity is a consequence of consumption which left insufficient litter biomass left to accumulate. Hall et al. (2006) reported that following high severity fire in ponderosa pine forests of the Colorado Front Range, it took 120 years for litter mass to stabilize. The initial reduction in duff was also persistent with losses in these sites approaching ~100%. Unlike low and moderately burned sites, the long-term accumulation of duff will be limited by litter input (Hall et al. 2006).

Surface woody fuel loads increased continuously throughout the 5 years postfire in high severity sites (Table 3.4). The initial 92% reduction of FWD recovered to unburned levels after 4 years. Similarly, initial reductions of CWD of 81% were diminished as early as the 3rd year postfire and exceeded levels in unburned stands by 74% at the end of the 5 years. The steady and rapid increase of both FWD and CWD is attributed to the accelerated fall rate of the fire-killed trees. After 5 years, ~61% of all trees >10 cm dbh had either completely fallen or were partially broken. This concurs with other postfire snag-fall studies that report ponderosa pine snag fall remains stagnant for 3-4 years postfire, but increases significantly 4-7 years postfire (Chambers and Mast 2005). Coarse woody debris in high severity sites already exceeds that of unburned stands and is ~115% greater than the average CWD load in the Black Hills of 14 Mg/ha (Reich et al. 2004). Given that ~80% of fire-killed trees fall or break within 10 years (Harrington 1996), continued accumulation of both FWD and CWD is expected.

Management implications

Little change in forest structure occurred as a result of low severity fire. These areas maintained full stocking and probably did not change forest growth patterns and, therefore, do not require artificial reforestation. In terms of fuels reduction efforts, the low severity surface fires, which occurred over 25% of the burned landscape, accomplished what most fuels reductions efforts are designed to do: reduce unnaturally high fuel loadings and the potential for severe fire behavior (Agee and Skinner 2005). While average HLC was not increased in low severity sites relative to unburned stands, a reduction in both FWD and CWD and duff mass may reduce flame lengths and fire severity in future wildfire or prescribed fire events which decreases the potential for torching and simplifies fire control efforts (Agee and Skinner 2005). The lack of mortality in the larger canopy trees, however, maintains a canopy fuels structure that may continue to be susceptible to crown fire under severe weather conditions (Agee and Skinner 2005, Keyes and O'Hara 2002).

Substantial fuel accumulation occurred throughout the 5 years following the Jasper fire following both moderate and high severity fire. While fire hazard in these sites is not of particular importance in the short-term (Brown et al. 2003), continued snag fall and fuel accumulation through the 10^{th} year postfire (Harrington 1996) will result in an increase in potential fire intensity and severity (Brown et al. 2003). These fire hazards will only escalate as fallen snags decay and transition from solid to rotten biomass throughout the following 30 years (DeBano et al. 1998, Passovoy and Fule′ 2006). Dominance of the fuel bed by rotten wood greatly increases ignitability, residence time, and contributes greatly to smoldering combustion (DeBano et al. 1998). This is of particular importance as it is during the smoldering process that smoke and particulate emissions are greatest and heat transfer through the mineral soil occurs greatly increasing the severity of fire effects on soil organisms and vegetation (DeBano et al. 1998). Five years postfire, the opportunities for fuels reduction treatments within these sites are limited. The creation of heavy slash fuels due to snag-fall creates a situation in which fuels reduction via prescribed fire is a high-risk option for forest managers. In addition, fire effects and fire behavior associated with heavy slash fuels would likely have negative impacts on forest soils and vegetation due to the increased severity of fire effects associated with high fuel loads (DeBano et al. 1998). Alternatively, models (e.g. FFE-FVS) suggest that postfire salvage operations during the immediate months postfire have the potential to limit CWD accumulation following high severity wildfire and reduce fire severity in future reburn events (McIver and Ottmar 2007).

Fire effects on the overstory and forest floor interact to influence the development of stands impacted by wildfire. In combination with increased light, reduced duff depth, increased PAN, and the presence of residual seed trees, we expected to see high rates of seedling germination, establishment, and growth within these low and moderate severity sites. Instead, seedling germination and establishment was sporadic and likely due to prolonged drought conditions following the fire (Fig. 3.4). Brown and Wu (2005) found prolific regeneration and recruitment of ponderosa pine prior to Euro-American settlement in southwestern Colorado occurred only when disturbances opened portions of the canopy concurrent with or followed by periods of adequate moisture. Given ample moisture in the future, we expect to see significant regeneration in low and moderate severity sites similar in amount to or exceeding that in unburned stands making any efforts to artificially stock these stands unwarranted.

A different scenario exists in areas that experienced active crown fire with high severity fire effects. Regeneration and overstory development following stand-replacing wildfire has been shown to vary considerably in ponderosa pine forests. Postfire development in to a late-successional, closed-canopied forest, shrubland, and grass/forb dominated meadows are successional trajectories that have all been documented following stand-replacing wildfire in the Southwest (Savage and Mast 2005). The return of these stands to a late-successional forest will be dependent upon patch size and proximity to seed source. As the patch size increases, the proximity to off-site seed sources increases and limits regeneration of heavy-seeded ponderosa pine to forest edges (Peterson and Carson 1996, Greene and Johnson 2000, Bonnet et al. 2005). The need to artificially plant these stands will need to be dealt with on a stand by stand basis and will ultimately depend on management goals and objectives. If postfire objectives include a rapid return of large high severity patches to the timber base, artificial planting will be required, especially in the 32% of high severity patches between 100-1000 ha (Lentile et al. 2005). However, along the guidelines of ecosystem management, returning stands to production is often not the primary goal as maintaining newly created wildlife habitat and increasing biodiversity becomes of important in postfire management plans. Prior to the Jasper fire, only 2% of the Black Hills landscape was classified as non-stocked (DeBlaner 2002); substantially less than the acreage noted by Graves prior to Euro-American settlement (1899). Allowing these stands to follow a natural successional trajectory increases structural heterogeneity and has the potential to maintain vegetation and cover types that are rare within this heavily managed forested landscape.

Conclusions

The monitoring of the Jasper fire over 5 years provided evidence that forest structure varies temporally as well as with the severity of initial fire effects following mixed-severity wildfires. Prior to the Jasper fire, the landscape was a homogeneous second-growth, closed-canopied ponderosa pine forest. Five years postfire, it is a heterogeneous landscape with a complex mosaic of different stand structures and cover types that developed as a result of different fire behavior and fire severity. Approximately 25% of the landscape experienced low severity surface fire which did not significantly alter overstory structure, but did result in a long-term change in the structure and composition of the forest floor. In contrast, the 48% of stands that burned under moderate severity surface fire coupled with individual tree torching are now open, low density stands consisting of only large diameter ponderosa pine. These stands do, however, have a woody fuel bed similar to that of the unburned forests. The 27% of the area that burned under high severity crown fire has experienced the most significant changes in both overstory and forest floor structure. Unless artificially stocked, these stands will remain open herbaceous/shrublands for decades (Savage and Mast 2005) and possess woody fuel loads above that of the surrounding forest.

The variation in overstory and forest floor structure associated with mixed-severity fire creates a challenge for land managers detailed to create and implement postfire management prescriptions. Our results suggest that postfire rehabilitation efforts need to vary in these mixed-severity type fire events. Appropriate responses include small-scale, stand-level based mitigation measures ranging from no action in areas of low severity fire to more intensive actions such as artificial planting in high severity areas. Longer-term monitoring, followed by communication of results, increases a manager's ability to make scientifically-based decisions regarding postfire management actions and provides managers insight into postfire forest structure and function and its relation to future timber production, wildlife habitat, and long-term planning objectives.

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List of Tables

List of Figures

Table 3.1. Description of fire severity classes based on indicators of fire behavior that occurred in ponderosa pine stands during the Jasper fire in the Black Hills, SD in late summer 2000. Fire severity classes follow Ryan and Noste's (1985) classification system and were reported in Lentile et al. (2005).

Fire severity class	Percent of landscape	Fire behavior	Indicators of fire behavior
Unburned	N/A	N/A	Sites located in adjacent unburned pine stands; serve as "preburn" reference point and basis for postfire recovery
Low	25	Surface fire	Litter and duff only partially consumed with no bare mineral exposed, <25% crown scorch with no crown consumption
Moderate	48	Surface fire with some individual tree torching	Majority of litter and duff consumed, >25% crown scorch with partial crown consumption
High	27	Active, stand replacing crown fire	Litter and duff completely consumed resulting in exposure of bare mineral soil,~100% of needles consumed

Table 3.2. Prefire (2000) and 5 year postfire (2005) stand structure (live trees ≥5 cm dbh) of unburned, low, moderate, and high severity ponderosa pine sites within the Jasper fire perimeter in the Black Hills, SD. Analyses of density data, BA, and PAR data were performed on $\log_e + 1$, square root, and arsin$\sqrt{}$ transformed data, respectively. Values represent the untransformed mean ± 1 SE. Means followed by the same letter are not significantly different within a column at $\alpha = 0.05$.

	Prefire				2005				
Fire Severity	Total density (trees/ha)	Total BA (m^2/ha)	ASD (cm)	HLC (m)	Total density (trees/ha)	Total BA (m^2/ha)	ASD (cm)	HLC (m)	PAR (%)
Unburned	727 ± 109	24.8 ± 1.1	21.8 ± 1.1	5.8 ± 0.6	714 ± 104^{a}	26.3 ± 1.0^{a}	22.6 ± 1.1^{a}	6.5 ± 0.6^{a}	36 ± 2^{a}
Low	667 ± 137	23.2 ± 2.5	22.5 ± 1.3	5.0 ± 0.6	474 ± 43^{b}	21.3 ± 2.1^{a}	24.2 ± 1.1^{a}	6.7 ± 0.7^{a}	51 ± 3^{b}
Moderate	521± 59	23.0 ± 2.1	24.3 ± 0.6	5.6 ± 0.5	190 ± 41^{b}	10.8 ± 2.0^{b}	27.6 ± 1.0^{b}	9.9 ± 0.5^{b}	68 ± 3^{c}
High	757 ± 86	24.1 ± 1.5	21.1 ± 1.0	5.9 ± 0.3	N/A	N/A	N/A	N/A	85 ± 2^{d}
Pr > *F*	0.2062	0.8782	0.1777	0.3632	<0.0001	<0.0001	0.0099	0.0003	<0.0001

Table 3.3. Litter mass (Mg/ha) and duff mass (Mg/ha) within unburned, low, moderate, and high severity ponderosa pine stands 1, 2, 3, 4, and 5 years (2001-2005) following the Jasper fire in the Black Hills, SD. Individual year analyses were performed after a significant Severity x Year interaction (P<0.05). Analyses of litter and duff mass were performed on square root transformed data. Values presented represent the untransformed mean ± 1 SE. Means followed by the same letter are not significantly different within a given year.

	Litter mass (Mg/ha)					Duff mass (Mg/ha)			
	2001	2002	2003	2004	2005	2002	2003	2004	2005
Unburned	16.1 ± 1.5^{a}	14.6 ± 1.3^{a}	15.9 ± 1.1^{a}	15.7 ± 1.2^{a}	16.3 ± 0.8^{a}	28.2 ± 2.6^{a}	22.4 ± 1.3^{a}	21.9 ± 1.6^{a}	25.2 ± 1.8^{a}
Low	5.1 ± 0.5^{b}	9.5 ± 1.1^{b}	10.5 ± 1.3^{b}	12.5 ± 0.7^{b}	12.3 ± 0.5^{b}	3.2 ± 1.3^{b}	3.4 ± 0.8^{b}	4.2 ± 0.6^{b}	5.5 ± 0.8^{b}
Moderate	2.0 ± 0.3^{c}	9.7 ± 1.3^{b}	11.1 ± 0.8^{b}	11.5 ± 0.7^{b}	10.4 ± 0.9^{c}	1.4 ± 0.8^{bc}	3.0 ± 0.5^{b}	3.0 ± 0.4^{b}	4.2 ± 0.8^{b}
High	1.3 ± 0.6^{d}	1.4 ± 0.3^{c}	2.9 ± 0.5^{c}	0.7 ± 0.2^{c}	1.1 ± 0.3^{d}	0.7 ± 0.7^{c}	0.4 ± 0.2^{c}	0.3 ± 0.2^{c}	0.3 ± 0.1^{c}
Pr > F	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Table 3.4. Surface woody fuel loadings (Mg/ha) for FWD and CWD within unburned, low, moderate, and high severity ponderosa pine stands 1, 2, 3, 4, and 5 years (2001-2005) following the Jasper fire in the Black Hills, SD. Individual year analyses were performed after a significant Severity x Year interaction ($P < 0.05$). Analyses of FWD and CWD were performed on the square root transformed data. Values represent the untransformed mean ± 1 SE. Means followed by the same letter are not significantly different within a given year.

	FWD (<7.62 cm) surface woody fuel load (Mg/ha)					CWD (>7.62 cm) surface woody fuel load (Mg/ha)				
	2001	2002	2003	2004	2005	2001	2002	2003	2004	2005
Unburned	5.9 ± 1.3[a]	5.3 ± 1.3[a]	6.9 ± 1.1[a]	10.1 ± 1.6[a]	10.2 ± 1.6[a]	14.0 ± 2.9[a]	14.6 ± 3.5[a]	14.8 ± 3.3[a]	15.4 ± 3.0	17.2 ± 3.2[a]
Low	2.1 ± 0.4[b]	2.5 ± 0.8[bc]	3.3 ± 0.6[b]	3.2 ± 0.8[b]	4.1 ± 0.7[b]	2.9 ± 1.0[b]	4.1 ± 2.1[b]	4.9 ± 2.8[b]	5.7 ± 1.6	6.7 ± 2.1[b]
Moderate	1.2 ± 0.3[bc]	2.7 ± 0.7[ab]	3.1 ± 0.6[b]	5.0 ± 1.4[b]	12.5 ± 3.3[a]	2.2 ± 1.3[b]	2.6 ± 1.2[b]	3.1 ± 1.5[b]	9.3 ± 3.9	19.8 ± 5.3[ac]
High	0.5 ± 0.2[c]	0.8 ± 0.4[c]	1.7 ± 0.6[b]	6.5 ± 1.6[ab]	14.1 ± 2.2[a]	3.4 ± 1.4[b]	6.5± 4.0[b]	6.0 ± 3.2[b]	14.1 ± 3.2	30.0 ± 3.1[c]
Pr>*F*	<0.0001	0.0052	0.0006	0.0057	0.0160	<0.0001	0.0164	0.0075	0.0605	0.0011

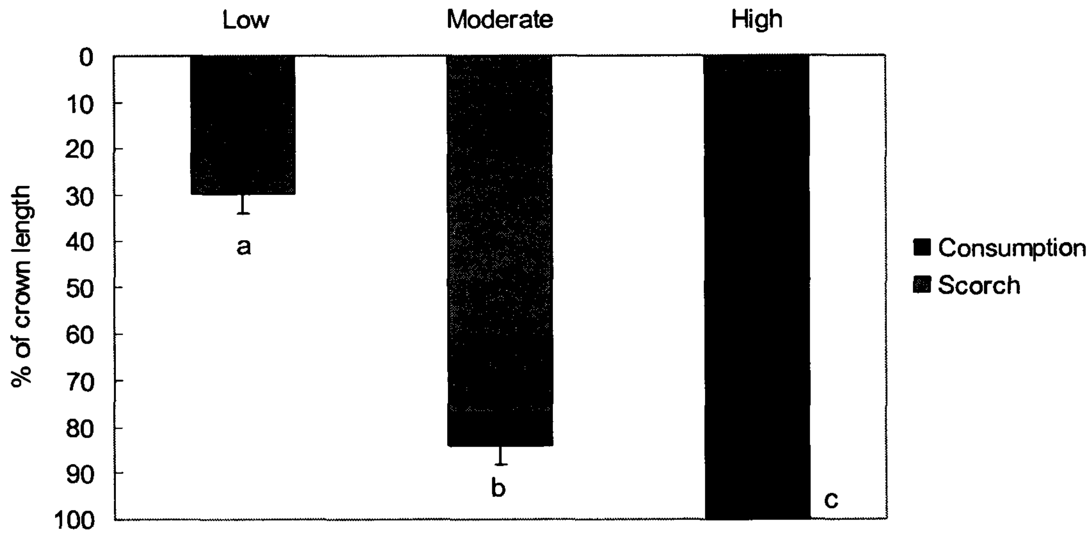

Fig. 3.1. Proportion of crown damage due to scorch and consumption following the Jasper fire in late summer 2000 in ponderosa pine stands impacted by low, moderate, and high severity fire in the Black Hills, SD. Total crown damage is the sum of crown scorch and consumption. Analysis of total crown damage data was performed on √arcsin transformed data. Different letters indicate statistical differences in total crown damage among fire severities at $\alpha = 0.05$. Values presented are the untransformed mean total crown damage ± 1 SE.

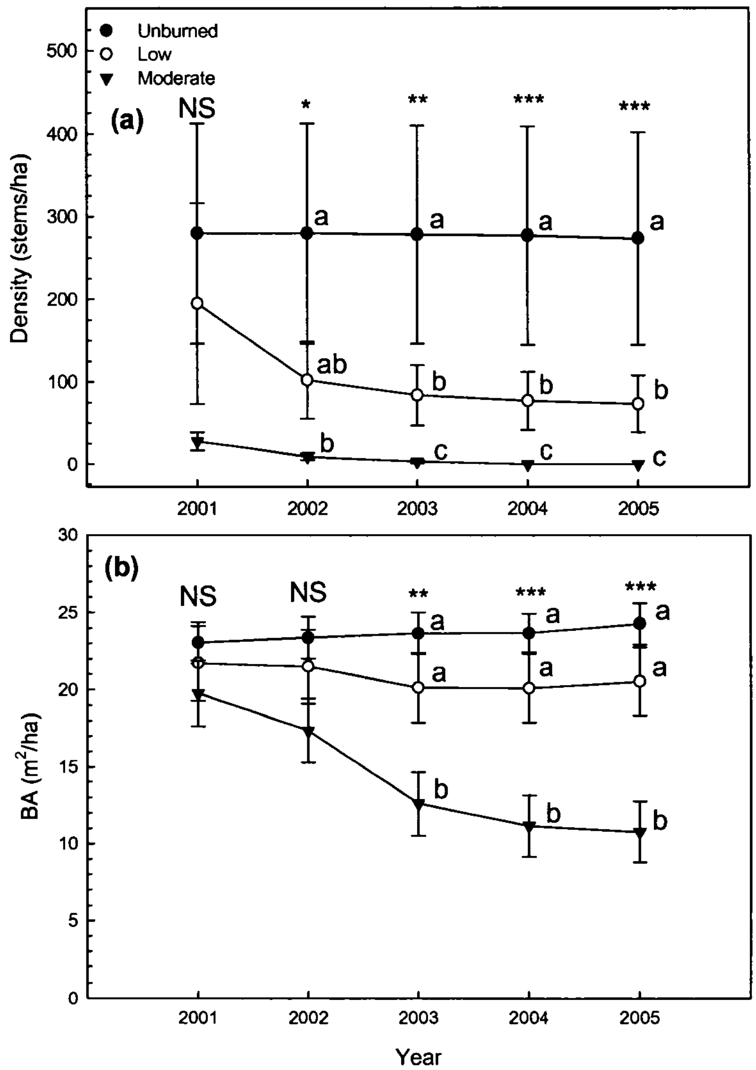

Fig. 3.2. **(a)** Density (live trees/ha) of trees ≥5 cm and <15 cm dbh and **(b)** BA (m^2/ha) of live trees ≥ 15 cm dbh in unburned, low, moderate, and high severity ponderosa pine sites within the Jasper fire perimeter in the Black Hills, SD 1, 2, 3, 4, and 5 years postfire (2001-2005). Individual year analyses were performed following significant Severity x Year interactions in the repeated measures analysis of density ($P < 0.05$) and BA (P<0.0001). Analysis of BA data was performed on square root transformed data and analysis of density data was performed on $\log_e + 1$ transformed data. Values presented are the untransformed mean ± 1 SE. Asterisks signify significance between severities within a given year: * P<0.05; **P<0.01; ***P<0.001; NS, not significant. Means followed by the same letter within a given year are not significantly different at $\alpha = 0.05$.

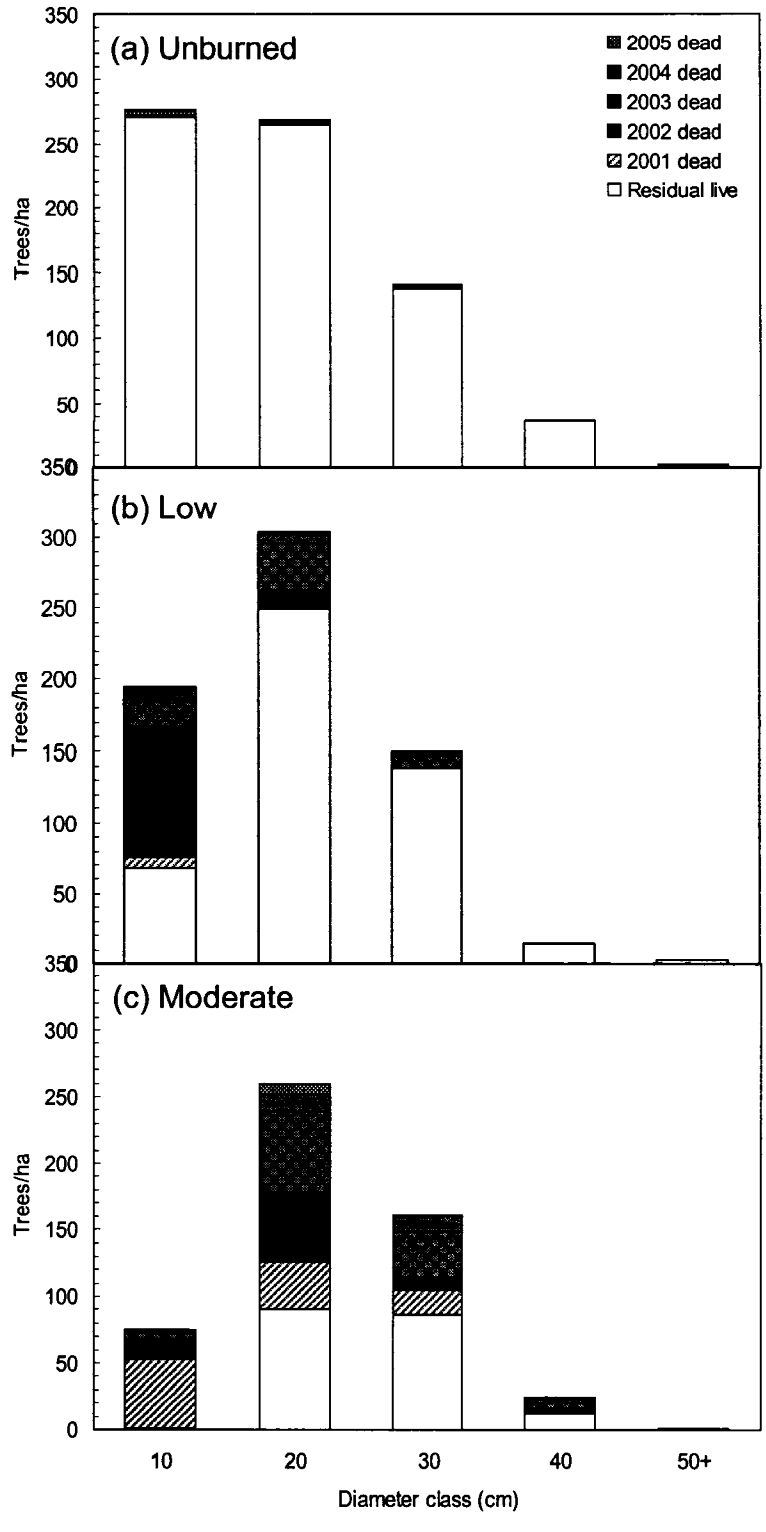

Fig. 3.3. Incremental and accumulated mortality by diameter class in ponderosa pine stands impacted by **(a)** unburned, **(b)** low, and **(c)** moderate severity in the Black Hills, SD 1, 2, 3, 4, and 5 years postfire (2001-2005).

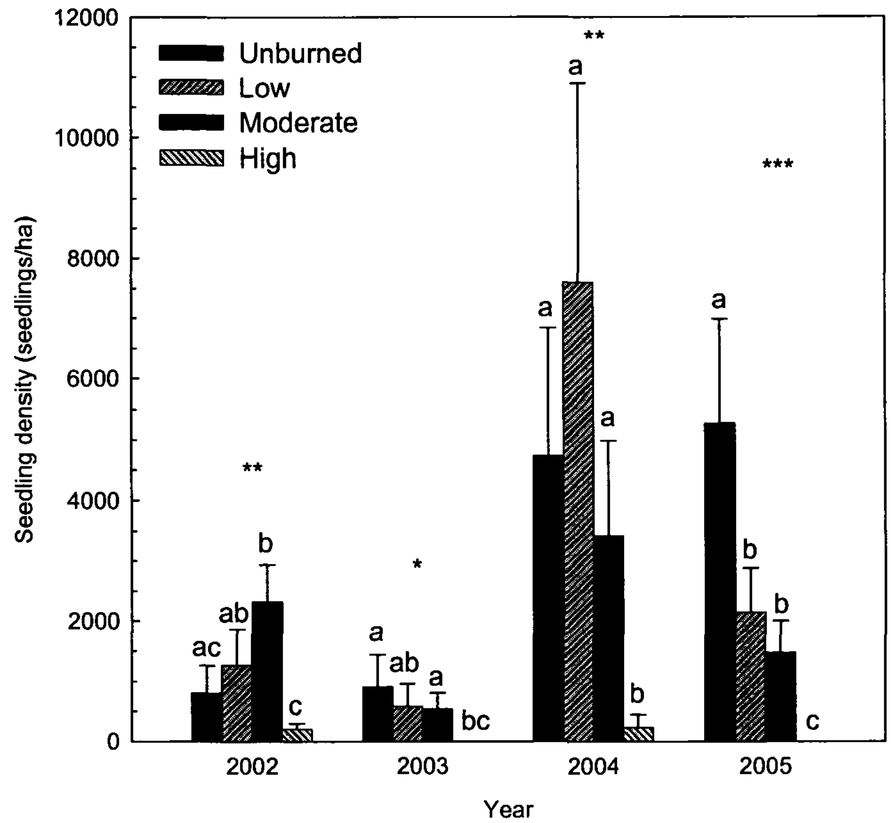

Fig. 3.4. Cumulative postfire regeneration density within unburned, low, moderate, and high severity ponderosa pine sites within the Jasper fire perimeter in the Black Hills, SD 1, 2, 3, 4, and 5 years postfire (2001-2005). Individual year analyses were performed following a significant Severity x Year interaction (P<0.0001) in the repeated measures analysis. Regeneration was not aged in 2001 and therefore not included. Analyses of seedling density data were performed on square root transformed data. Values presented in the figure represent the untransformed mean ± 1 SE. Asterisks signify significance between severities within a given year: *P<0.05; **P<0.01; ***P<0.001; NS, not significant. Means followed by the same letter within a given year are not significantly different at $\alpha = 0.05$.

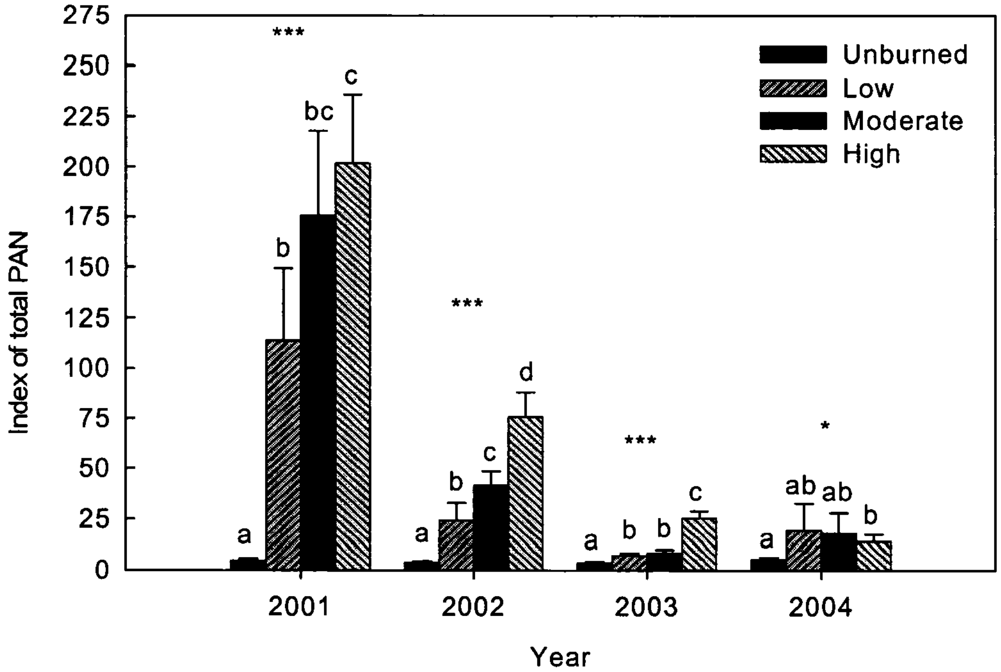

Fig. 3.5. Total PAN calculated as available $NO3^{-2}$ + available $NH4^{+}$ within unburned, low, moderate, and high severity ponderosa pine sites inside the Jasper fire perimeter in the Black Hills, SD 1, 2, 3, 4, and 5 years postfire (2001-2005). Individual year analyses were performed following a significant Severity x Year interaction ($P<0.0001$) in the repeated measures analysis. Analyses of total nitrogen data were performed on $\log_e + 1$ transformed data. Values presented in the figure represent the untransformed mean ± 1 SE. Asterisks signify significance between severities within a given year: *$P<0.05$; **$P<0.01$; ***$P<0.001$. Means followed by the same letter within a given are not significantly different at $\alpha = 0.05$.

IV. TEMPORAL CHANGES IN UNDERSTORY COMMUNITY STRUCTURE AND SPECIES COMPOSITION FOLLOWING A LARGE, MIXED-SEVERITY WILDFIRE IN PONDEROSA PINE FORESTS OF THE BLACK HILLS, USA.

ABSTRACT

Wildfires alter forest understory plant communities by removing fire-intolerant species and modifying the competitive growing environment. Following mixed-severity wildfires, the degree of departure in the forest understory from prefire or unburned conditions varies in relation to the severity of direct fire effects. In this study, w examined the effects of fire severity on the recovery of understory vegetation structure (e.g. distribution of cover among functional groups: grasses, forbs, and shrubs) and species composition throughout the 5 years following a mixed-severity wildfire in ponderosa pine (*Pinus ponderosa* Laws.) forests of the Black Hills, SD, USA. The Jasper fire burned ~34,000 ha of the Black Hills National Forest during late summer 2000 and was characterized by variable patterns of fire behavior containing elements of low severity surface fire, moderate severity surface fire with some torching, and high severity active crown fire. Fire severity had an immediate and significant impact on both understory structure and composition that lasted throughout the 5 years postfire. Compared to the unburned stands, there was an immediate reduction in total plant cover, regardless of fire severity; however these

differences were nonexistent after only 2 years. While total cover recovered quickly, understory structure was significantly altered. Based on our unburned stands, prior to the Jasper fire, the forest understory was a shrub dominated system with common juniper (*Juniperus communis*) making up ~15% of the ~50% total cover. Five years postfire, low severity sites differed only in the amount of shrub cover making these sites most similar in terms of structure to unburned stands; however low severity sites contained a significantly different species composition than unburned sites. Deviations in structure and composition were more dramatic following moderate and high severity fire as 5 years postfire these sites were now dominated by forbs and grasses making not only structure different, but species composition as well. An undesired consequence of more severe fire was an increase in exotic plant cover in moderate and high severity sites. However, noxious or invasive weeds accounted for only 4 and 2% of total exotic plant cover in moderate and high severity sites.

INTRODUCTION

While often viewed as catastrophic events, mixed-severity wildfires in which fire behavior varies along a continuum from low severity surface fire to high-severity active crown fire (Lentile et al. 2005) can increase heterogeneity throughout the forest understory vegetation by removing fire-intolerant species (Schoennagel et al. 2005, Agee 1993) and altering growing conditions. Following fire, overstory tree mortality which increases canopy light transmittance (Hale 2003) and reduces competition for water, nutrients, and light (Reigel et al. 1995) along with increased nutrient availability and the exposure of bare mineral soil interact to influence the postfire competitive environment. Recovery of understory vegetation from wildfire can be especially complicated following mixed-severity fires where fire effects, patch size, distance to unburned edges, and postfire propagule availability (Lee 2004, Turner et al. 1997) are highly variable. In this paper, we evaluate the effects of fire severity on the recovery and development of understory structure and species composition over a 5 year period in ponderosa pine (*Pinus ponderosa* Laws.) forests of the Black Hills, South Dakota and compare the processes of understory recovery in areas impacted by low, moderate, and high severity fire.

Ecological succession and community development following wildfire is influenced by patch size, which can vary from 1 ha to >1000 ha in mixed-severity fires (Lentile et al. 2005), and postfire propagule availability. The amount of influence patch size has on the recovery of understory vegetation, however, varies in relation to fire severity. Low severity surface fire is often patchy and can cause incomplete consumption of litter, duff, and vegetation (Knapp and Keeley 2006). Because of this patchiness, legacy plants that survive or resprout postfire exert a strong influence on postfire recovery patterns (Knapp and Keeley 2006, Foster et al. 1998). Laughlin et al. (2004) observed that species composition in ponderosa pine stands burning under low-severity surface fire were most similar to unburned reference stands, suggesting that species either resprout following fire or are fire survivors that provide a within site seed source. Patch size has a strong control over postfire development in areas that experience moderate e.g. high severity surface fire with torching) and high (e.g. active crown fire) severity fire due to the consumption of understory vegetation and mortality within the soil seed bank. As moderate and high severity patch size increases, distance to an outside seed source increases (Klinger et al. 2006) restricting the propagule pool to those species capable of vegetatively reproducing (Lee 2004).

The postfire environment has a substantial impact on the re-establishment and growth of understory vegetation (Covington and Sackett 1992). Increased nutrient availability along with decreased competition for water and light interact to influence species composition and abundance. Reduced competition and increased nutrient availability is dependent upon fire severity. Mixed-severity fires are characterized by spatially variable patterns of fire severity, patch size, and overstory mortality (Lentile et al. 2005, Agee,1993). For ponderosa pine, tree mortality increases with increased fire severity (Keyser et al. 2006, McHugh and Kolb 2003, Stephens and Finney 2002). The reduction in tree density and canopy cover associated with tree mortality increases canopy light transmittance (Comeau 2006, Hale 2003) as well as reduces below-ground competition for water and nutrients between the herbaceous/shrub understory and the overstory trees (Spurr and Barnes 1980). Functional groups respond differently to increases in light and water availability, which occur concurrently following fire. For example, in ponderosa pine forests of the Southwest, abundance and productivity of herbaceous vegetation (e.g. grasses, sedges, and forbs) increase in response to reduced overstory density whereas the response by shrubs is often considerably less (Moore and Deiter 1992). In addition, to changes in the relative abundance of individual functional groups, species composition (Bataineh et al. 2006) within groups is modified with the alteration of resources (Reigel et al. 1995). Batanieh et al. (2006) concluded that while species composition did not differ among all unburned, low, and high severity sites immediately following fire in ponderosa pine forests of northern Arizona, low and high severity fire ultimately caused long-term (>30 years) differences in species composition. Structural changes (e.g. reduced tree density and decreased canopy cover) may not be immediately apparent following fire as mortality is not usually complete until 3 to 4 years post-fire (Keyser et al. 2006, Agee 2003, Ryan et al. 1988). Therefore, understory vegetation recovery and development may be dynamic process spanning a longer period of time than direct fire effects remain visible (Betaineh et al. 2006).

Increased understory production observed following wildfire in ponderosa pine (Moore et al. 2006, Keeley et al. 2003, Pearson et al. 1972) is attributed to the low competition, high resource environment of postfire habitats. Unfortunately, an increasing proportion of the recovering understory comes from the establishment of non-native species. Numerous studies have documented an increase in the abundance of exotic species in postfire environments with more severe disturbance (e.g. fire severity) resulting in greater establishment of exotic species (Griffis et al. 2001). Following a wildfire in northern Arizona, Crawford et al. (2001) reported a significant increase in the abundance of exotic species with increased litter and duff consumption. Exotic species have also been shown to respond to the increased nutrient availability in postfire environments. Gundale et al. (2006) reported that of six species that responded positively to increased nitrogen availability following a restoration treatment in ponderosa pine forests in northern Montana, four were considered exotic. The combustion of organic matter (e.g. litter, duff, and woody biomass) increases nutrient availability throughout the immediate years postfire.

Plant available nitrogen (PAN) has been shown to increase immediately following fire (Prieto-Fern´andez et al. 2004, Deluca and Zouhar 2000). This increase in PAN is proportional to the amount of organic matter consumed (White 1986) so that increased fire severity and fuel consumption increases PAN (Smithwick et al. 2005). Exotic species establishment in mixed-severity fires is not well documented throughout the geographic range of ponderosa pine. Most information regarding species invasion is isolated to prescribed fires or high-severity fire in the Southwest and provides little guidance in developing postfire rehabilitation plans to control noxious weeds following mixed-severity wildfire.

Information regarding ecological succession and understory development following fire in ponderosa pine forests is not as developed as in other forest types due, in part, to the variability in fire behavior that can occur within these ecosystems. In this study, we document 5 years of postfire change in understory vegetation composition and structure to study the impact of mixed-severity wildfire in ponderosa pine dominated forests of the Black Hills. Specifically, we used 5 years of monitoring data to (*i)* examine changes in the recovery and persistence of functional groups (e.g. forbs, graminoid, and shrubs) following low, moderate, and high severity fire, (*ii*) evaluate the impact of fire severity on understory species composition through time, and (*iii*) investigate whether the establishment of exotic species varies in response to fire severity.

METHODS

Study area

The study was located within the Jasper fire perimeter in the Black Hills National Forest, South Dakota, USA (latitudes between 43° 42' and 43° 57' and longitudes between 103° 46' and 104° 1'). The Black Hills are an isolated, forested uplift that extend ~190 km in the north-south direction and ~60-80 km in the east-west direction (Froiland 1990). This dome-shaped uplift rises between ~900-1200 m above the surrounding Great Plains in southwestern South Dakota and northeastern Wyoming (Hoffman and Alexander 1987) and form the easternmost extent of the Rocky Mountains (Froiland 1990). Dominant soils are similar throughout the area and are mainly Alfisols, Mollisols, and Inceptisols (Shepperd and Battaglia 2002). The climate is continental with cold winters and mild, moist summers (Johnson 1949). Mean maximum and minimum daily temperatures range from -3.3 and 13.2 and yearly precipitations averages ~47 cm with 65-75% occurring between the months of April and October (Shepperd and Battaglia 2002, Froiland 1990, Hoffman and Alexander 1987).

On August 24, 2000, the Jasper fire was ignited near the town of Custer, SD. The fire was contained on September 8, 2000 after burning ~34,000 ha or ~7% of the Limestone Plateau area of the Black Hills National Forest (Shepperd and Battaglia, 2002, USDA 2000). The Jasper fire was a mixed-severity fire that produced a combination of surface fire (low fire behavior), surface fire with torching (moderate fire behavior), and active crown fire (extreme fire behavior) that burned through predominantly second-growth ponderosa pine (Lentile et al. 2005). The patterns of fire behavior left behind a mosaic of low, moderate, and high severity fire effects across the landscape (Lentile et al. 2005).

Experimental design

In the months following the fire, in collaboration with Black Hills National Forest staff, we identified from postfire aerial photographs 3 – 800 ha forest units in which no postfire silvicultural activities (e.g. salvage harvesting) would occur. The three units had each experienced a combination of low, moderate, and high fire behavior. In June 2001, we randomly established 36 – 0.3 ha permanent study sites in burned and unburned ponderosa pine stands within and adjacent to the Jasper fire perimeter. Sites were established in a complete block design with forest unit serving as the block and fire severity serving as the treatment. Each block contained 3 replicates of each fire severity class. Twenty seven of the 36 sites were located in ponderosa pine stands that exhibited evidence of having burned under different types of fire behavior. Sites were established within treatments or fire severity classes which we assigned based on the indicators of fire behavior reported by Lentile et al. (2005) and Keyser et al. (*in review*). Within the burned stands, 9 sites were located in areas exhibiting evidence of surface fire behavior (treatment = low severity), 9 sites were located in stands exhibiting evidence of moderate fire behavior consisting of surface fire with individual tree torching (treatment = moderate severity), and 9 sites were located in areas exhibiting evidence of active, stand-replacing crown fire (treatment = high severity). The remaining 9 sites were located in adjacent unburned pine stands and served as our control sites (treatment = unburned).

We recognize that using adjacent unburned sites as a basis for comparing fire effects on the forest floor and soil nitrogen requires that we assume no differences existed between the burned and unburned sites prior to the fire. This assumption is appropriate given the similarity in prefire stand structure among the burned and unburned ponderosa pine stands. Numerous studies (e.g. Fule′ et al. 2004) have used adjacent unburned stands as a proxy for prefire controls for studying fire effects on existing vegetation.

Data collection

We sampled all vegetation using 6 – 0.5 m^2 understory plots per site in one (2001), two (2002), three (2003), and five (2005) years postfire. All understory vegetation plots were sampled during mid-summer (late June through early August) to control for seasonal changes in understory composition. Understory vegetation plots were located every 10 m, 20 m, and 30 m east and west of the 60 m transect that ran through each site center for a total of six plots per site. Within each of the 0.5 m^2 vegetation plots, we measured understory vascular plant cover and species composition. Ponderosa pine seedlings <1.4 m in height (dbh) were included in the understory sampling and categorized as shrubs. Cover of each species was averaged for each site. In addition, in 2002 we destructively samples 10 individuals of each identified species off-site and determined the percent of each species that germinated via seed or resprouted following the fire. All nomenclature as well as native and non-native status of species follows the USDA NRCS PLANTS database (USDA 2006). The vast majority of vascular plants possessed characteristics that allowed us to identify them down to the species level. However, instances arose when vegetative characteristics were insufficient to identify species. In those cases, plants were identified to the genus level.

At each site we measured environmental variables including basal area (BA) mortality, litter and duff mass, below-canopy light transmittance (CLT; %), and plant available nitrogen (PAN) annually from 2001 to 2005. In addition, we measured the proportion of each site that possessed low, moderate, and high severity ground char effects in 2001. Methods regarding the collection of these data as well as results are reported in Keyser et al. *(in review)*.

Multivariate analyses

We used non-metric multi-dimensional scaling (NMS) to visually display how sites align in space relative to species composition 1, 2, 3, and 5 years following the Japer fire. Non-metric multi-dimensional scaling is a multivariate technique that iteratively arranges *n* sites in *k*-dimensional space such that sites with similar species composition are close together and pairs of sites that differ in species composition are farther apart (McCune and Grace 2002). Ordination results that produce inter-site differences or stress values <20 are considered useful in evaluating community ecology data (McCune and Grace 2002). We used the Bray-Curtis (Sørenson's) distance measure as a measure of dissimilarity among sites and the slow and thorough autopilot to produce the ordination. The autopilot process determines the best *k*-dimensional ordination based on 40 real runs, 50 randomized runs, a maximum of 400 iterations, and an instability criterion of 0.00001. A Monte Carlo test based on 50 randomized runs is then used to determine the probability of achieving a similar ordination by chance alone. Varimax rotation was utilized to maximize the alignment of environmental measures of fire severity with axis 1. We used relativized data in which species occurring on less than 5% of the sites were removed for all multivariate analyses because we were interested in differences in species assemblages rather than total abundance (McCune and Grace 2002).

The multi-response permutation procedure (MRPP) using the Bray-Curtis distance measure was used to test for differences in species composition among fire severities within a given year (α=0.05). The MRPP procedure is a non-parametric analysis similar to an analysis of variance (ANOVA), however, MRPP does not assume normality or homoscedasticity within species data (McCune and Grace 2002). The method produces a statistic and *p*-value similar to the *F*-statistic in an ANOVA by analyzing species composition is more alike within fire severities than predicted by chance. The MRPP procedure does not accommodate our replicated block design; therefore, prior to the analyses, we ran a preliminary NMS ordination to visually assess whether there were differences in species composition among sites from the southern, central, and northern locations (e.g. blocks). Based on the NMS ordination, we did not identify any grouping patterns in species composition among the three forest units. Subsequently, we took the more conservative approach of removing the block factor in order to find test for differences in species composition among the fire severities. The MRPP and NMS routines were performed using PC-Ord version 5.0 (MjM Software Design, Glendon Beach, Oregon).

When a useful NMS ordination was produced (final stress < 20) and significant differences occurred following MRPP, we used indicator species analysis (ISA) to find the most common species within each fire severity class and year. Only species that have an indicator value (INDVAL) >25 and a *P*-value < 0.05 (calculated on Monte Carlo Monte Carlo randomizations with 10000 permutations) were considered indicator species of a particular fire severity (Dufrêne and Legendre 1997). The INDVAL statistics is the product of the relative abundance and relative frequency of a species within a fire severity (Dufrêne and Legendre 1997).

Repeated measures analyses

Changes in total cover, cover summarized by functional group (i.e. shrub, forb, and grass) and non-native cover were analyzed as a repeated measures ANOVA to determine the effects of fire severity and time (1-5 years postfire) on postfire understory recovery. Covariance structures for the repeated measures analyses were modeled as either a first-order autoregressive model or a first-order autoregressive model with heterogeneous variances with site included as a random variable. Separate ANOVAs were performed to test the impact of fire severity each year because the repeated measures analysis indicated significant severity x year interactions for all response variables. Following significant F-tests, pairwise multiple comparisons of ls-means among fire severities were performed using the Fisher's LSD procedure (Steel et al. 1997). Fire severities were significantly different at $\alpha = 0.05$. Response variables were collected as percent plant cover, therefore data were arc sin square-root transformed to achieve normality and homoscedasticity (Steel et al. 1997). The means and standard errors we report are the raw, untransformed data. Analyses of cover data were performed using SAS v. 9.1 (SAS Institute 2005).

RESULTS

Understory cover

Variability in burn severity led to substantial impacts on the forest floor. Using Ryan and Noste's (1985) ground effects classification system, low severity sites experienced the least amount of severe fire effects throughout the forest floor followed by moderate and high severity sites (Table 4.1). The impacts of fire severity on the forest floor led to significant impacts on forest vegetation. Immediately following the Jasper fire, we found significant reductions in total plant cover relative to the unburned controls, regardless of fire severity (Fig. 4.1a). The impact of fire severity on total plant cover was as expected with lower rates of forest floor consumption in low severity sites resulting in a ~16% decrease in total cover and total consumption of the forest floor in high severity sites resulting in a ~30% loss in total cover. The initial reductions in total cover within each fire severity class varied over a short amount of time (F = 11.8, df = 9, 31.2, P < 0.0001) such that by 2 years postfire, the differences in total cover observed immediately postfire were not detectable.

While total cover quickly recovered within all burned sites, the distribution of cover among the functional groups (e.g. forbs, grasses, and shrubs) varied depending upon fire severity. Forb cover was significantly impacted by fire severity, however the relationship between forb cover and fire severity varied with recovery time (F = 5.9, df = 9, 53.2, P < 0.0001). Differences in forb cover among fire severities were not observed until 2 years postfire when forb cover in moderate severity sites was 14% greater than that in unburned stands (Fig. 4.1b). After 3 years, forb cover in both moderate and high severity sites was, on average, 24% greater than the forb cover in unburned and low severity sites Stands that burned under moderate and high severity fire continued to have increased forb cover relative to unburned sites 5 years postfire at which time forb cover in moderate and high severity sites was 18 and 29% greater than in unburned sites and 14 and 25% greater than in low severity sites. Of all forb species present in 2002, 54% resprouted following the fire and 46% germinated via seed.

Fire severity also had a significant impact on the reestablishment of grasses, however the relationship between grass cover and fire severity varied throughout the 5 years following the fire ($F = 8.6$, df = 9, 64, $P < 0.0001$). Unlike forb cover, differences in grass cover as a result of fire severity were observed as early as 1 year postfire (Fig. 4.1c). One year postfire, grass cover in unburned, low and moderate sites was similar, but grass cover was negligible in high severity sites. By the 2nd year postfire, 22% of the ground cover consisted of various graminoid species however grass cover in high severity was still <5% and remained lower than grass cover in the unburned and the less severely burned sites. By the 5th growing season postfire, grass cover had recovered to unburned levels in all burned sites regardless of fire severity. Within burned sites, however, grass cover was 16% greater in moderate severity sites than in unburned and high severity sites and 11% greater than in low severity sites. Of all grass species present in 2002, 84% resprouted following the fire and 16% germinated via seed.

The initial response of shrubs to fire severity and the long-term recovery of shrub cover within burned sites varied with fire severity and year since fire ($F = 4.2$, df = 9, 62.6, $P = 0.0003$). One year postfire, shrub cover was, on average, 22% lower in burned sites than in unburned sites (Fig. 4.1d). Shrub cover increased between 1 and 2 years postfire, but after 2 years was still, on average, 18% lower in burned sites than in unburned sites. By the 3rd year postfire, shrubs in high severity sites had recovered to unburned levels. After 5 years, shrub cover in low and moderate severity sites remained 13% and 17% lower than in unburned stands. Shrubs were the most likely to sprout. Of all shrub species present in 2002, 86% regenerated by sprouting and only 12% germinated from seed.

The Jasper fire had a significant impact on the establishment and growth of exotic species, however the effect of fire severity on total exotic cover varied within individual years ($F = 7.7$, df = 9, 40.4, $P < 0.0001$). Following individual year ANOVAs, we were able to detect significant differences in exotic plant cover among the fire severities by the 2nd year postfire (Fig. 4.2). Total exotic cover at this time was low regardless of fire severity averaging ~5%. Exotic cover remained low through the 3rd year postfire but after 5 years increased substantially in moderate and high severity sites accounting for 20 and 13% of total cover.

Ordination analysis

Differences in relative understory community composition 1, 2, and 5 years postfire were determined using NMS ordination. A useful ordination was not found for the data collected during the 3rd year postfire (final stress >20) and therefore not displayed. A 3-dimensional ordination that explained 61% of the total variance in species composition among sites was chosen for the data 1 year postfire (final stress = 18.97, final instability < 0.0001, P-value = 0.0040; Fig. 4.3a). After rotation of the axes around the BA mortality, axis 1 was most closely correlated with the BA mortality ($r^2 = 0.33$), proportion of the site with heavy ground char ($r^2 = 0.31$), duff mass (r^2 = -0.25), and litter mass (r^2 = 0.25). Unburned sites were clustered together in space and associated with high amounts litter and duff. No distinct grouping pattern was visible in low and moderate severity sites which is likely due to limited tree mortality immediately postfire. In contrast, high severity sites were clustered and associated with areas of high mortality of overstory trees and heavy ground char.

A 4-dimensional ordination explained the variation in species composition amount sites 2 years postfire (final stress = 14.35, final instability < 0.0001, *P*-value = 0.0040; Fig. 4.3b) with the first three axes explaining 46% of the total variation. Axis 1 and axis 3 accounted for 29% of the variation. After varimax rotation, Axis 1 was positively correlated with BA mortality (r^2 = 0.41), PAN (r^2 = 0.25), and heavy ground char (r^2 = 0.20). Axis 3 was positively correlated with duff mass (r^2 = 0.18) and negatively correlated with moderate ground char (r^2 = 0.39) Again, unburned and high severity sites formed distinct groups in which species composition among sites was associated with average duff depth, BA mortality, and available nitrogen.

A 3-dimensional ordination explained 64% of the variation in species composition among sites 5 years postfire (final stress = 18.17, final instability < 0.0001, *P*-value = 0.0040; Fig. 4.3c). In the 2005 ordination, axis 1 and axis 3 accounted for ~50% of the variation in species composition among sites. After rotation, axis 1 was positively correlated with BA mortality (r^2=0.38), PAR (r^2=0.36), and moderate ground char (r^2=0.34) while negatively correlated with litter mass (r^2 = -0.24) and duff mass (r^2=0.37). By the end of the 5th year postfire, unburned, low, moderate, and high severity sites had all formed distinct grouping patterns. Species composition in unburned and low severity sites was determined, in part, by litter and duff mass whereas species composition in moderate and high severity sites was associated with BA mortality, PAR, and the percent of the site with moderate severity ground char.

The MRPP analysis supported the trends and groupings observed in the NMS ordinations. We found significant differences in species composition among fire severities 1, 2, and 5 years postfire ($P < 0.001$). Regardless of fire severity or year since fire, burned sites possessed significantly different species composition patterns than unburned sites (Table 4.2). Within burned sites, however, differences among the fire severities differed yearly. One year postfire, only species assemblages found in low and high severity sites were significantly different. By the 2nd year postfire, species composition in low and moderate severity sites was significantly different than in high severity sites, but not from each other. At the end of the 5 years, species composition in all burned sites, regardless of fire severity was significantly different.

Species characteristic of unburned, low, moderate, and high severity sites were derived from the indicator species analysis (Table 4.3). Unburned sites possessed the greatest number of indicator species 1, 2, and 5 years postfire. Three species consistently associated with unburned sites included fire intolerant species such as common juniper (*Juniperus communis*; Tirmenstein 1999) and fire surviving species (via sprouting) such as the shrub bearberry (*Arctostaphylos uva-ursi*; Crane 1991) and the forb starry false Solomon's seal (*Maianthemum stellatum*; Habeck 1992). By the 2nd year postfire, indicator species were identified in low, moderate and high severity sites. Low severity sites were identified by the presence of the graminoid Richardson's sedge (*Carex richardsonii*). Two forbs characterized moderate severity sites during this year including the exotic species prickly lettuce (*Lactuca serriola*) and native species bunchberry (*Cornus canadensis*). Forbs species including American dragonhead (*Dracocephalum parviflorum*) and purple milkvetch (*Astragalus agrestis*) were indicative of high severity sites 2 years postfire. At the end of the 5 years, species composition in moderate severity sites continued to differentiate. However, 3 out of the 5 indicator species within these sites were exotic species including Kentucky bluegrass (*Poa pretense*), common dandelion (*Taraxacum officinale*), and the noxious weed Canadian thistle (*Cirsium arvense*).

DISCUSSION

The Jasper fire burned as a mixed-mode fire creating a mosaic of initial fire effects across a 34,000 ha landscape. While much of this landscape burned under high severity active crown fire (39%), significant proportions also burned under moderate (32%) or low (24%) fire behavior (USDA 2000). The patterns of fire severity observed during and immediately after the Jasper fire were influenced by heterogeneity in prefire stand conditions and topography (Lentile et al. 2006). Patch sizes formed by each fire severity were variable but ~1/3 of the patches formed by low, moderate, and high severity fire were between 100 and 1000 ha (Lentile et al. 2005). While some patch sizes were >1000 ha (Lentile et al. 2005), the fine-scale mosaic of fire severities across the landscape provide for sufficient living edge and potential seed sources throughout the burned area. Substantial differences in species composition and subsequent recovery of the understory vegetation within these second-growth ponderosa pine forests resulted from variability in the severity of direct fire effects. Differences in the rate and amount of recovery following mixed-severity fires have important implications regarding postfire management actions, in particular whether or not there is an immediate need for postfire rehabilitation such as aerial seeding applications intended to control postfire erosion and limit the establishment of exotic and noxious weed species (Beyers 2004, Robichaud et al. 2000).

Regardless of fire severity, differences in total cover present immediately following the Jasper fire were not detected by the end of the second growing season. This rapid return of total cover and understory productivity following fire is typical of the understory vegetation in ponderosa pine ecosystems. Gildar et al. (2004) found that following prescribed fire, understory vegetation cover returned to and in some sites exceeded the total cover in the unburned sites in relic ponderosa pine stands in northern Arizona. Similarly, Wienk et al. (2004) found that following cutting and burning treatments total understory production surpassed untreated levels 2 growing seasons post-treatment citing reduced overstory density as well as increased light, soil moisture, and soil temperature as possible mechanisms driving recovery. They also noted that sites with complete overstory removal, like our high severity sites and to a less extent our moderate severity sites, showed the greatest response in understory production. Cover (Huisinga et al. 2005) and productivity (Bataineh et al. 2006) of burned forests may continue to increase over long time periods (e.g. 5-30 years) following high intensity/severity wildfire. Continued availability of limiting resources such as light and soil moisture along with increased soil temperatures

(Bonnet et al. 2005) will likely continue to promote understory development in the more severely burned areas of the Jasper fire.

While total cover recovered to unburned levels quickly, dominance by functional groups changed dramatically relative to unburned sites depending upon fire severity. Unburned sites were dominated by shrubs throughout the 5 years postfire accounting for over 50% of the total cover followed by forb and grass species (Fig. 4.1). By the end of 5 years, none of the burned sites, regardless of fire severity, were dominated by shrubs and only high severity sites had shrub cover values similar to unburned sites. The rapid return of shrub cover to unburned levels following high severity fire is likely due to decreased competition for water, light, and nutrients due to the loss of overstory vegetation (Riegel et al. 1995, 1992). The quick response of shrubs to high severity fire following the Jasper fire, however, contradicts other studies that show a significant lag in the recovery of shrubs following high severity fire. For example, compared to unburned sites, Turner et al. (1999) observed significantly lower shrub cover in high severity fires 4 years following the 1988 wildfires in Yellowstone National Park. Similarly, Wienk et al. (2004) found no response of shrub productivity to either burning and (or) the reduction of overstory density in ponderosa pine forests of the Black Hills. However, Schoennagel et al. (2004) report that shrub cover increases steadily with time since fire and that a quick recovery can occur if shrub species are rapidly sprouting species. The dominant shrub species present in burned sites after the Jasper fire, regardless of fire severity, were species from the genus *Symphoricarpos* and *Amalenchier alnifolia*; both of which are prolific sprouters capable of surviving even high-intensity wildfire

(Howard 1997, Esser 1995). Absent from burned sites was the fire-intolerant species common juniper (Tirmenstein 1999) which was common throughout unburned sites contributing to an average of ~15% of ~50% total cover in these sites.

Forbs responded significantly with increasing fire severity. By the end of the 5-year monitoring period, forb cover was increased, relative to unburned sites, in areas impacted by moderate and high severity fire, but not in low severity sites (Fig. 4.1b). Forbs have been shown to respond significantly to reductions in overstory density. Moore and Deiter (1992) reported a significant negative relationship between stand density index (SDI), which takes into account tree size as well as stand density, and forb production. Keyser et al. (*in review*) have shown that significant reductions in large tree density, and hence SDI, occurred only in moderate and high severity sites following the Jasper fire. Many perennial, fire-tolerant forb species possess meristems and storage organs deep in the soil layer and therefore are not damaged by even high severity fire allowing them to regenerate vegetatively immediately following fire (Schoennagel et al. 2004). The rapid postfire sprouting of forb species immediately following wildfire allows for the capture resources at the expense of slower sprouting species or obligate seeders enabling these species to out-compete their competitors. Environmental variables such as the minor reduction in stand density, incomplete consumption of vegetation, litter, and duff, and reduced light levels in found in low severity sites (Keyser et al. *in review*) likely slowed the development of forb cover within these sites limiting forb cover similar to that of unburned sites.

Grasses fill an ecological as well as economic niche within the management goals of the Black Hills. Grasses are seasonally important for wildlife species such as the white-tailed deer (*Odocoileu virginianus*) and are the preferred forage utilized by grazing cattle (Uresk and Severson 1989). As with other functional groups, the recovery of grass cover to unburned levels was strongly influenced by fire severity and time since fire (Fig. 4.1c). By end of the 5 years, grass cover in low and high severity sites was equal to unburned levels, however grass cover in moderate severity sites exceeded that in unburned sites. The response of grass species to overstory conditions is similar to that found in forbs. In general, as overstory density and tree size increase, competition for water, nutrients, and light among understory and overstory species increases (Riegel 1995, 1992). As this competition for resources diminishes due to postfire tree mortality, more resources become available for understory vegetation, in particular grass species. The increase in grass cover associated with areas of high tree mortality following the Jasper fire is in agreement with models developed for the Black Hills predicting understory productivity as related to stand structure. Uresk and Severson (1989) report a significant relationship between stand BA and grass production in ponderosa pine forests of the Black Hills with stands possessing between 0 and 14 m^2/ha of BA having greater grass production than stands with >14 m^2/ha. At the end of the 5-year monitoring period, BA in moderate and high severity stands averaged 11 and 0 m^2/ha, respectively; well within the range predicted to increase grass production. Low severity sites which have >20 m^2/ha of BA fall within the range of unthinned stands which as predicted by

Uresk and Severson (1989) typically show decreased or, at most, sustained grass production.

Regardless of fire severity, the Jasper fire had a significant impact on understory plant community and floristic composition throughout the 5 year monitoring period. At no point in time during this study did plant composition in burned sites resemble species composition characteristic of the unburned sites (Table 4.2). In addition, the similarities observed between low and moderate severity sites as well as moderate and high severity sites were ameliorated by the 5^{th} year postfire making species composition significantly different among all the fire severities. Similar trends in floristic composition have been documented following mixed-severity wildfires in Southwestern ponderosa pine forests. For example 2 years postfire, Crawford et al. (2001) reported that stands which had undergone unburned, moderate, and high severity fire possessed a low mean similarity index which resulted in significant differences in community composition among all fire severities. The divergence in understory composition from unburned sites has been documented in few long-term studies that have examined the impact of wildfire on understory vegetation. Following a 1971 mixed-severity wildfire in northern Arizona ponderosa pine forests, Bataineh et al. (2006) documented that even after 30 years, significant differences in species composition still existed between low severity and unburned stands and high severity and unburned stands. The divergence in community composition suggests a long-term shift in species composition within stands impacted by low, moderate, and high severity fire.

In conjunction with shifts in species composition away from that found in unburned stands, specific species are now associated with and a viable indicator of sites that burned under low, moderate, or high fire severity throughout the Jasper fire landscape (Table 4.3). Indicator species analysis found numerous species that were indicative of unburned sites meaning that the species were either specific to only unburned sites or always present in unburned sites. Indicators of unburned sites were either fire-intolerant in that they were readily killed by fire without the ability to rapidly resprout, such as common juniper, or possess life history characteristics that allowed them to survive in low-light, undisturbed habitats. No single species could be used an indicator of stands that had experienced low severity fire, perhaps due to species overlap between low severity and unburned sites because of the incomplete consumption of prefire vegetation. With the exception of unburned sites, only one species, desert stickweed, was captured as an indicator species in high severity sites in multiple years. This suggests that species dominance and species composition are still, after 5 years, changing dramatically through time making predictions about future composition difficult.

While the indicator species analysis did not identify any exotic species that identified high severity sites, moderate severity sites could be identified by the presence of exotic species. During the early years postfire, the contribution of exotic species to overall plant cover was low (Fig. 4.2). While total cover recovered to unburned levels after 2 years, this did not deter the establishment of exotic species. Environmental conditions including significant bare ground (Crawford et al. 2001), high nutrient availability (Gundale 2006), and decreased competition for above- and below-ground resources (Busch and Smith 1995, D'Antonio et al. 1991) in moderate and high severity areas (Keyser et al. *in review*) made these sites conducive to the establishment and reproduction of exotic species such that after 5 years exotic plant cover was greater in the more severely burned sites than unburned sites. The increase in exotic species with increased levels or severity of disturbance is well documented. For example, Griffis et al. (2001) observed that while species abundance increased from low intensity prescribed fire to a stand-replacing wildfire in southwestern ponderosa pine forests, a significant proportion of that increase came as a result of the establishment of exotic species sites. While exotic plant cover increased, the majority of the exotic species were not noxious with most species such as common dandelion and Kentucky bluegrass considered naturalized. The only noxious species of concern following the Jasper fire was Canada thistle which was present in relatively low cover values in moderate and high severity sites contributed to only ~4 and 2% of the total cover, respectively. While the increased presence of Canada thistle is an unfortunate result of the fire, a study by Travnicek et al. (2005) suggests that increased Canada thistle densities commonly observed following fire may be short-lived making extensive efforts (e.g. herbicide application) to control the relatively insignificant establishment of this species an uneconomical and (or) non-ecological alternative.

Conclusions

Prior to the Jasper fire, the understories of these second-growth ponderosa pine forests were shrub dominated systems. The lack of fire during the last century along with timber management activities facilitated the establishment and growth of juniper such that prefire, it accounted for ~35% of the shrub cover and ~20% of the total vegetative cover within these stands. After 5 years, the distribution of functional groups within the 25% of the landscape that burned under low severity fire (Lentile et al. 2005) most closely resembled unburned stands however, the lack of juniper in the understory and significant changes in species composition contribute to the subtle differences between unburned and low severity stands. Both understory structure and composition within the 48% and 27% of the landscape impacted by moderate and high severity fire (Lentile et al. 2005) were substantially altered from the surrounding unburned forest. After 5 years, moderate and high severity stands were dominated by forbs and grasses providing an increase in the quantity of herbaceous forage for wildlife as well as domestic livestock. The high rates of consumption coupled with high overstory mortality following moderate severity fire and 100% mortality following high severity fire created environmental conditions (e.g. increased PAN and decreased above- and below-ground competition; Keyser et al. *in review*) that will maintain the structural and compositional diversity within these sites well into the future. In moderate severity stands, the dominance by forbs and grasses will likely continue until a closed-canopied forest develops (Ursek and Severson 1989) at which time, shrubs, in particular juniper, may once again dominate the understory. In contrast, in the larger patches of high severity fire, a closed-canopied forest will not likely develop resulting in a change in cover type from forest to a grass/forb dominated meadow (Savage and Mast 2005). These differential patterns of understory recovery within low, moderate, and high severity fire will ultimately result in a long-term increase in structural and compositional heterogeneity within a relatively homogeneous surrounding landscape.

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List of Tables

List of Figures

Table 4.1. Percent of low, moderate, and high severity ponderosa pine sites with unburned ground and low, moderate, and high severity ground effects immediately following the Jasper fire in the Black Hills, SD. Ground char classification based on methods developed by Ryan and Noste (1985).

Fire severity	Unburned (%)	Low severity char (%)	Moderate severity char (%)	High severity char (%)
Low	18	49	29	3
Moderate	0	32	48	19
High	0	3	43	52

Table 4.2. Comparisons of understory species composition among unburned, low, moderate, and high severity ponderosa pine sites in the Black Hills, SD following a significant MRPP analysis (*P*<0.05) 1, 2, and 5 years following the Jasper fire.
** Species composition is significantly different at α=0.05 within a given year.

Fire severity	2001	2002	2005
Unburned vs low	0.008**	0.027**	0.001**
Unburned vs moderate	0.004**	<0.001**	<0.001**
Unburned vs high	<0.001**	<0.001**	<0.001**
Low vs moderate	0.600	0.233	0.045**
Low vs high	0.009**	<0.001**	0.003**
Moderate vs high	0.090	0.001**	0.005**

Table 4.3. Indicator species analysis for unburned, low, moderate, and high severity ponderosa pine stands within the Jasper fire perimeter for years in which a useful NMS ordination (final stress<20) and significant MRPPs ($P < 0.05$) were produced (1, 2, and 5 years following the Jasper fire). Asterisks signify *exotic species, **exotic and noxious species.

Year	Fire severity	Species	Indicator value	*P*-value
2001	Unburned	*Symphoricarpos sp.*	53	0.0023
		Juniperus communis	44	0.0095
		Pinus ponderosa	64	0.0009
		Rosa sp.	68	0.0003
		Arctostaphylos uva-ursi	46	0.0093
		Phlox hoodii	35	0.0450
		Maianthemum stellatum	40	0.0086
		Lathyrus ochroleucus	56	0.0011
	Low	NONE		
	Moderate	NONE		
	High	NONE		
2002	Unburned	*Elytrigia repens**	49	0.0038
		Antennaria parvifolia	33	0.0470
		Rosa sp.	57	0.0009
		Fragaria virginiana	33	0.0486
		Juniperus communis	44	0.0077
		Maianthemum stellatum	33	0.0472
		Lathyrus ochroleucus	44	0.0097
		Arctostaphylos uva-ursi	40	0.0219
		Pinus ponderosa	58	0.0034
	Low	*Carex richardsonii*	35	0.0216
	Moderate	*Lactuca seriola**	47	0.0102
		Cornus canadensis	41	0.0156
	High	*Astragalus agrestis*	54	0.0013
		Dracocephalum parviflorum	41	0.0175
2005	Unburned	*Arctostaphylos uva-ursi*	56	0.0015
		Juniperus communis	33	0.0449
		Rosa sp.	40	0.0363
		Pinus ponderosa	55	0.0050
		Carex sp.	49	0.0036
		Maianthemum stellatum	49	0.0018
		Geum triflorum	33	0.0480
	Low	NONE		
	Moderate	*Cerastium arvense*	45	0.0089
		*Poa pratense**	40	0.0424
		*Taraxacum officinale**	55	0.0035
		Achillea millefolium	48	0.0390
		*Cirsium arvense***	40	0.0265
	High	*Amalanchier alnifolia*	46	0.0315
		Dracocephalum parviflorum	33	0.0484
		Camelina microcarpa	43	0.0234

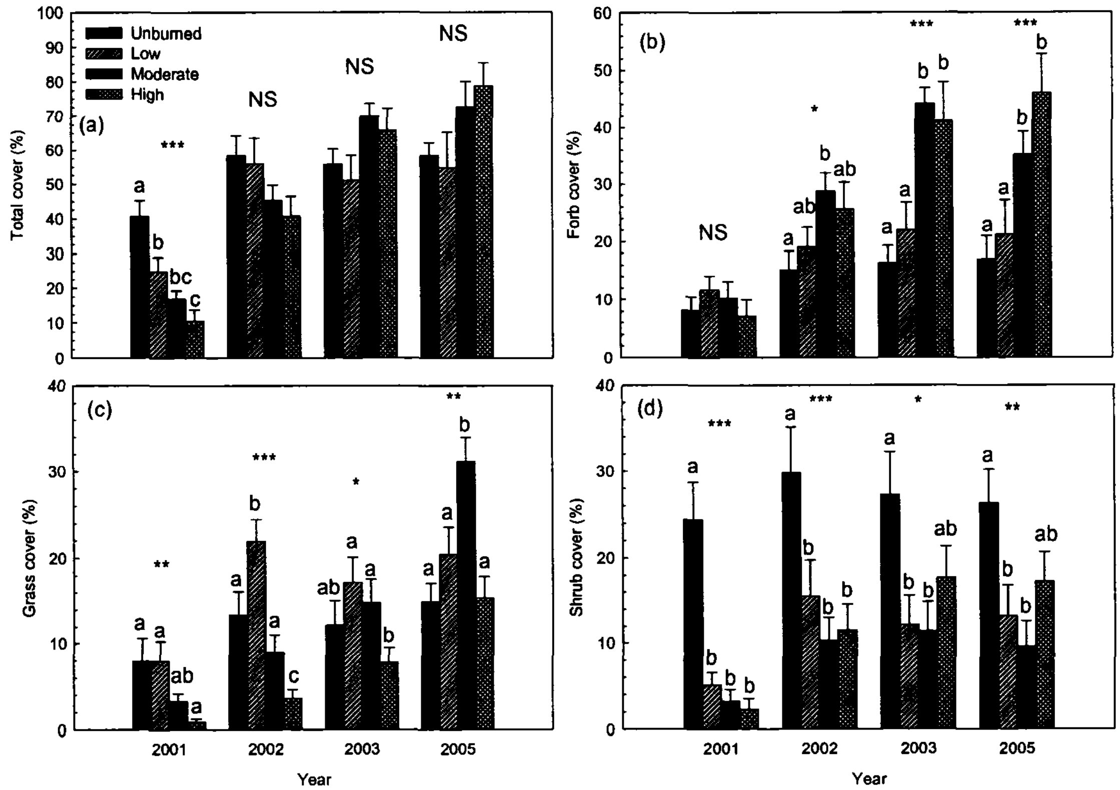

Fig. 4.1. **(a)** total cover (%) **(b)** forb cover (%), **(c)** grass cover (%), and **(d)** shrub cover (%) in unburned, low, moderate, and high severity ponderosa pine sites 1, 2, 3, and 5 years (2001-2005) following the Jasper fire in the Black Hills, SD. Individual year analyses were performed following significant severity x year interactions in the repeated measures analysis of cover data ($P < 0.05$). Analyses of cover data were performed on arcsine square root transformed data. Values presented are the untransformed mean ± 1 SE. Asterisks signify significance between severities within a given year: * $P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS, not significant. Means followed by the same letter within a given year are not significantly different at $\alpha = 0.05$.

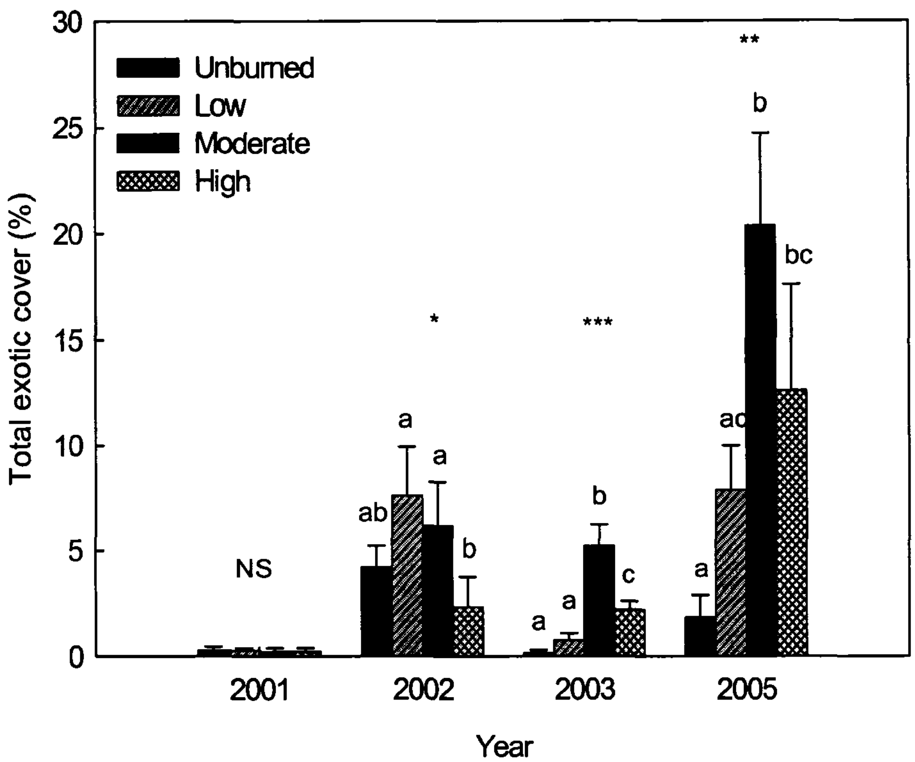

Fig. 4.2. Exotic species cover (%) in unburned, low, moderate, and high severity ponderosa pine sites 1, 2, 3, and 5 years (2001-2005) following the Jasper fire in the Black Hills, SD. Individual year analyses were performed following significant severity x year interaction in the repeated measures analysis of cover data ($P < 0.05$). Analyses of cover data were performed on arcsine square root transformed data. Values presented are the untransformed mean ± 1 SE. Asterisks signify significance between severities within a given year: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; NS, not significant. Means followed by the same letter within a given year are not significantly different at $\alpha = 0.05$.

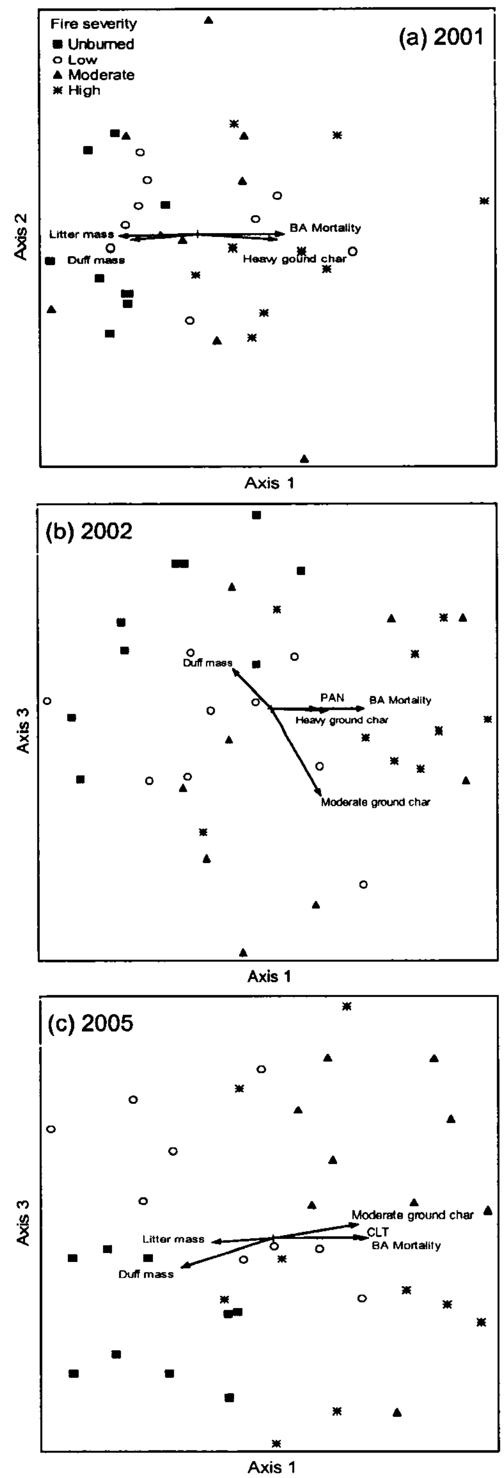

Fig. 4.3. Non-metric multidimentional scaling (NMS) of relativized cover data for understory plant species following the Jasper fire in the Black Hills National Forest, SD in **(a)** 2001, **(b)** 2002, and **(c)** 2005. Ground char ratings were based on the classification system presented in Ryan and Noste (1985). In all graphs, axis 1 was rotated to maximize correlation with BA mortality.