DISSERTATION

CAUSAL FACTORS AND CONSEQUENCES OF MIXED- SEVERITY FIRE IN BLACK HILLS PONDEROSA PINE FORESTS

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY LEIGH B. LENTILE ENTITLED CAUSAL FACTORS AND CONSEQUENCES OF MIXED- SEVERITY FIRE IN BLACK HILLS PONDEROSA PINE FORESTS BE ACCEPTED AS FULLFILING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

We used the ~34,000 ha Jasper fire of 2000 to address the theme of mixed-severity fire in Black Hills ponderosa pine forests. Mixed severity fire resulted in many patches of low, moderate, and high severity, distributed in roughly equal proportion across the burned landscape. There was a significant effect of stand structure and topography on burn severity despite the extreme weather conditions during the Jasper fire. Relative density, tree size, and slope, ranked in order of importance, were influential in predicting burn severity. Relative density < 40 % and slope < 18 % represent critical thresholds where low and moderate severity were more likely to occur. High stand density presented the most likely scenario for crown or high severity fire. Our conclusion that structure does influence burn severity has important implications in terms of fuels management and in understanding patterns of vegetation that influence burn severity even in events occurring during extreme weather conditions.

The Jasper fire left a landscape imprint distinct from other recent, large, western wildfires (e.g. the Yellowstone fires, WY, 1988, the Hayman fire, CO 2002, the Rodeo-Chedeski fire, AZ 2002, and the Biscuit fire, OR and CA, 2002). Rather than small patches of surviving vegetation in a matrix of crown fire, we observed small patches of crown fire interspersed among large patches of surviving vegetation. We inferred variable fire effects on aspects of canopy, understory plant communities, forest floor, and soil and differential rates of recovery to be the result of different burn severity. Tree mortality increased from ~1 to 16 % and 18 to 59 % in low and moderate severity patches during the first 3 years post-fire. All trees were killed in high severity patches. Greater reductions in plant cover were seen with greater severity. Herbaceous cover and richness recovered to pre-burned levels in all burned areas within three years post-fire. Fire initially removed aboveground shrub components, independent of severity, although shrub cover was ~ 40 % of pre-burn cover in high severity areas three years post-fire. Pre-fire species composition was highly influential in determining post-fire species composition, and we found ~ 70 % of species regenerated vegetatively. We found three times more non-native plant species following fire. Soil nitrogen availability was 21 and 41 times greater in areas of low and high severity than in unburned areas, but decreased two years post-fire. Tree mortality and associated changes in light transmission are ongoing in areas with surviving trees. Tree regeneration was limited and variable in the first three years post-fire. Many small patches of low, moderate, and high burn severity with a high proportion of surviving vegetation accelerated rates of recovery in the Jasper fire compared with other recent and large western fires.

Fire histories in ponderosa pine *(Pinus ponderosa var scopulorum)* forests are reconstructed from fire scar and tree origin information. Fire frequency, severity, and size are inferred from dates of fire occurrence as recorded as scars on individual trees and from cohort origin and structure. However, little is known about rates of fire scar formation in relation to burn severity and stand conditions, and critics have proposed a modern calibration to validate sampling and interpretation of fire history evidence. We examined tree mortality, incipient fire scar formation and ponderosa pine regeneration in patches of low, moderate, and high burn severity 2-3 years post-fire. Two years post-fire, tree mortality was ~ 6, 24 and 100 % in low, moderate and high burn severity. Three years post-fire, tree mortality had increased to ~ 21 and 52 % in areas of low and moderate burn severity. Two years post-fire, we examined ~ 2100 live trees for evidence of dead cambium within low and moderate severity patches. Dead cambium on a significant portion of tree circumference in a tree with live cambium and a vigorous crown was taken as evidence of incipient fire scar formation. Dead cambium was detected on ~ 24 and 44 % of surviving trees in low and moderate burn severity patches. Regeneration densities were ~ 531, 796, and 11 seedlings ha^{-1} in low, moderate, and high severity patches two years post-fire. Three years post-fire, regeneration densities were ~ 612 and 450 seedlings ha^{-1} in low and moderate severity patches, and we observed no regeneration in high severity patches. Tree-dominated cover may not return to the interior of large patches where the distance to seed source exceeds ponderosa pine seed dispersal distance for a long time. The pattern of future fire-scarred trees and post-fire cohorts that resulted from the Jasper fire is indicative of a mixed- severity fire regime consistent with fire history reconstructions in Black Hills ponderosa pine forests.

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I. INTRODUCTION

Ponderosa pine *(Pinus ponderosa var scopulorum)* forests in the Black Hills have a long history of utilization and anthropogenic influence (Alexander 1987; Shepperd and Battaglia 2002). Discovery of gold by the Custer expedition in the 1870's was followed by rapid Euro- American settlement of the area. During the late 1800's, large tracts were commercially clearcut in the absence of regulation to provide mining timber and railroad ties. The establishment of the Forest Reserve in 1897 imposed minimum diameter harvest controls and required retention of seed trees. In the first half of the 20th century, the shelterwood reproduction and individual tree selection methods were employed across large areas to capture anticipated mortality. Beginning in the 1960's and continuing to present, the two-cut shelterwood method has been used with timing of the removal cut based on understory establishment and development. As a result, nearly all of the unreserved and operable forests have been harvested at least once, and many twice, since Euro- American settlement (Boldt and Van Deusen 1974; Alexander 1987; Shepperd and Battaglia 2002).

Almost all of the old- growth pine forest in the Black Hills has been converted to an intensively managed second- growth forest (Boldt and Van Deusen 1974; Alexander and Edminster 1981). Current forests have lower diversity and higher tree densities, in particular, of small trees and saplings, when compared to historical forests. Understory plant biomass and species richness have likely declined as a result of increases in ponderosa pine canopy cover, trampling by cattle, and fire suppression. Snag densities and large, downed woody biomass have decreased as timber removal has occurred over most of the forest. Smaller woody biomass or fine fuel volume and continuity have increased over much of the forest with effective fire suppression. Increases in density and extent of ponderosa pine forests have resulted in a reduction in productivity and numbers of interior prairies and meadows, and a simplification of vegetative diversity and forest structure (USDA 1996).

Controversy exists regarding the role of fire in the maintenance of historical forest conditions. Dendrochronologically- based fire studies from drier and more open sites in the southern Black Hills suggest that low intensity, surface fires burned every 10 to 30 years (Brown and Sieg 1996, 1999). Extended wet conditions likely promoted tree regeneration, fast growth, and longer periods between surface fires, apparently reducing the likelihood for crown fires to burn in historical forests (Brown 2003). Shinneman and Baker (1997) suggest longer mean fire-return intervals and large, crown fires may have been important aspects of the disturbance regime in other parts of the Black Hills. In the northern and central Black Hills, extensive stand replacing fires (e.g. 1735, 1790, 1842, 1888, and 1890) created large areas of even-aged forest (Graves 1899; Shinneman and Baker 1997). In the 1899 forest inventory survey report, H.S. Graves wrote that patches of forest ~100 years old could be found everywhere in the Black Hills. Graves (1899) described multiple cohort stands with older, badly scarred, decadent trees, short in stature with full crowns that appear to have regenerated in very open conditions following a large fire. Variability in disturbance regimes appears to be related to climatic, topographical, and associated productivity differences in the Black Hills (Shinneman and Baker 1997; Brown et al. 2000; Shepperd and Battaglia 2002; Brown 2003).

The lack of surface fires to limit pine regeneration and the harvest of larger, older, and more fire- resistant trees has resulted in a feedback to the fire regime (Brown 2003). Contemporary fires are probably more extensive and severe than most historical fires due to current forest condition and extended drought. However, several large fires have been documented in the post-European settlement era. In the1890's, two large fires burned ~31,000 ha in the northern Black Hills, and in the 1930's the Rochford and McVey Fires burned ~17,000 ha on the Limestone Plateau. Each of these fires was described as wind-driven and fatal to nearly all the standing timber (USDA 1948). Since 2000, seven fires have burned ~ 60,000 ha, including large areas of both privately- and publicly- managed forests and grasslands. Undoubtedly, current forest landscape structure has been influenced by both large, stand-replacing, crown fires and by small, low-intensity, surface disturbances. For this reason, contemporary Black Hills fire regimes may be best described as mixed- severity, and efforts to restore attributes of both surface and small-scale crown fire are appropriate within the historical range of variability for interior forests.

Mixed- severity fire regimes have been least described perhaps due to the complexity inherent in the study of variable severity at multiple temporal and spatial scales (Brown and Smith 2000). Mixed- severity fire regimes may be the result of fine-scale, topographically-influenced differences in vegetation and fuel moisture that cause low- and high- severity fires to burn in proximity, although this transition is poorly understood (Fulé et al. 2003). Mixed- severity fire regimes in the Black Hills have described large, severe fires that occurred at longer intervals within interior forests and less severe, surface fires that burned more frequently in the ecotone between forest and prairie (Brown and Smith 2000). Severity may also vary within a single fire depending on complex interactions of weather, vegetation, and topography (Rowe and Scotter 1973; Wright and Heinselman 1973; Lyon and Stickney 1974; Van Wagner 1983; Turner et al. 1994) and produce a wide range of local effects on vegetation, forest floor, and soil resources. Mixed- severity fires create irregular burning patterns and produce a fine-grained pattern of stand structure and fuels, thereby, increasing the likelihood that these stands will burn again in mixed severity.

Causal factors and consequences of mixed- severity wildfires have raised important questions following the fire season of 2000, in which the Jasper fire, the largest fire in Black Hills recorded history, burned ~ 7 % of the forest in eight days. The Jasper fire exhibited variable burn severity and created a mosaic of vegetative mortality across the landscape. In Chapter II, we provide a description of fuel and weather conditions leading up to and during the Jasper fire and describe the imprint of this fire in areas with different structural characteristics and topographic features. While the overall proportion of the Jasper fire that burned at a given severity was most likely related to extreme weather conditions, the variation in the proportion of burn severity during a day was not caused by weather. There was a significant effect of stand structure and topography on burn severity under severe weather conditions. Our conclusion that structure does influence burn severity has important implications in terms of fuels management and in understanding patterns of vegetation that influence burn severity even in events occurring during extreme weather conditions.

This mixed- severity fire left a landscape imprint distinct from other recent, large, western wildfires. Rather than small patches of surviving vegetation in a matrix of crown fire, we observed small patches of crown fire interspersed among large patches of surviving vegetation. In Chapter III, we investigated direct and secondary fire effects in areas of low, moderate, and high burn severity. Pre-fire species composition was highly influential in determining post-fire species composition, and we found a majority of species regenerated vegetatively. Tree mortality and associated changes in light transmission are ongoing in areas with surviving trees. Tree regeneration may occur in low severity patches when favorable conditions for seed production and germination coincide, but will likely not persist due to high canopy density. Regeneration in moderate severity patches may emerge into the overstory due to high light and reduced canopy density. Regeneration may form dense, even-aged cohorts in high severity patches within the effective seed dispersal distance for ponderosa pine (30 m). Interior areas of high severity patches outside the effective seed dispersal distance may form persistent shrub communities and tree-dominated cover may not return to these areas for a long time. The juxtaposition of patches of low, moderate, and high severity likely accelerates recovery in large mixed- severity fires. Long interval, large-scale, mixed- severity fire events may be critical in maintaining landscape heterogeneity and diversity in Black Hills forests.

And, lastly, in Chapter IV, we asked how might this fire be interpreted by future fire historians based on fire scar and tree- ring evidence. Baker and Ehle (2001) criticized current interpretations of fire history based on fire-scarred tree analysis, and called fore a modern "calibration" of the fire scar record. A major issue in attempting modern calibration of historical fire regimes is that 20th century fire exclusion may have produced a more homogenous forest structure with increased tree densities and greater duff accumulations, and a concomitant increase in burn severity (Covington and Moore 1992, 1994a, 1994b). The Black Hills has not been immune to anthropogenic influence and significant changes since European settlement in landscape-scale processes and structure have occurred (Fisher et al. 1987; McAdams 1995; Brown and Sieg 1996; Shinneman and Baker 1997; Brown and Sieg 1999; Grafe and Horsted 2002). However, we documented significant differences in fire scar formation and establishment of post-fire seedling cohorts in relation to burn severity. Even if larger areas may burn at higher severity today than in the past, the effects of low, moderate, and high- severity fire probably were similar in historical fires to the effects we documented in the 2000 Jasper fire. All of our predictions are consistent with reconstruction of historical fire effects in the Black Hills, i.e., that fire burned at variable severity, creating a mosaic of variable canopy mortality and post-fire seedling recruitment (Brown and Sieg 1996, 1999; Shinneman and Baker 1997).

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II. CAUSAL FACTORS OF MIXED– SEVERITY FIRE IN BLACK HILLS PONDEROSA PINE FORESTS

ABSTRACT

Weather, forest structure and composition along with landscape position interact to determine a fire's severity. We used the ~34,000 ha Jasper fire of 2000 to address the theme of mixed- severity fire in Black Hills ponderosa pine systems. Mixed- severity fire resulted in many patches of low, moderate, and high severity, distributed in roughly equal proportion across the burned landscape. In this paper, we examined the influence of weather, topography, and pre-fire vegetative conditions on burn severity. We analyzed hourly weather conditions during eight days of active burning, pre-fire structural data from the Resource Inventory System (RIS), and topographical information from the 30-m Digital Elevation Model for the Black Hills. Weather conditions were extreme at times, and 60 % of the fire burned in < 12 hours. While the overall proportion of the Jasper fire that burned at a given severity was most likely related to extreme weather conditions, the variation in the proportion of burn severity during a day was not caused by weather. There was a significant effect of stand structure and topography on burn severity under the severe weather conditions during the Jasper fire. Relative density, tree size, and slope, ranked in order of importance, were influential in predicting burn severity. Relative density < 40 % and slope < 18 % represent critical thresholds where low and moderate severity were more likely to occur. Perhaps more importantly, we also

identified scenarios that were more likely to result in high burn severity. High stand density presented the most likely scenario for crown or high- severity fire. Stands with high density (RD > 40 %) comprised of larger trees (ASD > 24 cm) or many small trees were likely to burn in high severity. High burn severity was probably more predictable in stands with large trees due to high canopy bulk density or in stands with many small trees due to low crown base heights. Our conclusion that structure does influence burn severity has important implications in terms of fuels management and in understanding patterns of vegetation that influence burn severity even in events occurring during extreme weather conditions.

INTRODUCTION

Weather, topography, vegetation type and structure, and natural fire breaks may cause variation in burn severity within a single event (Rowe and Scotter 1973; Wright and Heinselman 1973; Van Wagner 1983; Van Wagner 1993; Turner et al. 1994). Fuels in whatever form cannot burn without an ignition source and the appropriate weather. The frequency of this weather determines the types of fire that burn and subsequently, the types of vegetation and fuels available for burning (Van Wagner 1983). Fire effects on vegetation may vary according to burn severity (Ryan and Noste 1985; Turner and Romme 1994; DeBano et al. 1998), and burn severity is largely driven by the dynamic interaction of fire behavior and fuels (Debano et al. 1998). For this reason, the concept of severity has been used to characterize fire regimes as low, high, and mixed. Fire regimes are often described by fire behavior that commonly occurs over a period of time. Burn severity and the additive effects from multiple fires influence vegetation composition, structure, and successional dynamics (Keane et al. 1990). The mixed- severity fire regime is characterized by fire behavior that kills some, but not all, of the aboveground vegetation, creating irregular patterns of fuels and stand structure (Brown and Smith 2000). Large-scale, mixed- severity fires often burn under changing weather conditions, cause variable effects on fuels and stand structure, and differentially impact certain areas of the landscape. Such events provide ideal opportunities for investigating the influence of weather, structure and topography on burn severity.

Causal factors and effects of mixed- severity wildfires have become a critical question in the Black Hills, SD, USA, following the fire season of 2000, in which 6 fires burned ~39,000 ha of ponderosa pine-dominated *(Pinus ponderosa var scopulorum)* forests and grasslands. The Jasper fire, like other recent, large wildfires (e.g. the Yellowstone fires, WY, 1988, the Hayman fire, CO 2002, the Rodeo-Chedeski fire, AZ 2002, and the Biscuit fire, OR and CA, 2002), exhibited variable burn severity and did not consume the entire forest. However, the landscape imprint of the Jasper Fire may be quite different from other large fires outside the Black Hills due to the prevalence of mixed-mode burning under extreme weather conditions. In this paper we describe burning patterns observed in the Jasper fire and describe the imprint of mixed- severity fire on the landscape. We also address the nature of this large fire, asking what caused the Jasper fire to burn in this way. An understanding of causal factors related to burn severity may be relevant to other large Black Hills fires and provide valuable insight for restoration efforts.

On the afternoon of August 24, 2000, the Jasper fire originated between Custer, SD and Newcastle, WY, and eventually burned across a heavily forested landscape dominated by gently dipping plateau ridges, dissected by steep, rocky canyons, and moderately sloping valleys. This fire was human-caused and spread rapidly, overpowering initial attack suppression forces. On the first day, the fire spread to the northeast, doubling in size every hour and consumed ~1500 ha within four hours. Almost immediately, the fire spread into the crowns of trees, and spot fires formed ahead of the main fire (JRAT 2000).

As day broke on August 26, the stage was set for what ultimately became the largest wildfire ever recorded in Black Hills history. During the afternoon, the fire developed into a plume-dominated fire, growing at an average rate of more than 40 ha min^{-1}. Over 18,000 ha of the BHNF was burned in a few short hours. By evening the convection column reached thunderstorm proportion, causing lightning and locally heavy rains outside the fire perimeter. Lightning from the firestorm started many fires that were suppressed in subsequent days (JRAT 2000).

The Jasper Fire was officially contained on September 8, 2000 after burning 33,795 ha or 7% of the BHNF land base. The rate of spread and extent of the Jasper fire surprised many managers and researchers. The Jasper fire spread rapidly through a variety of habitats under varying topographic conditions both in open meadows and in stands of different composition, age, structure, and density. The fire was initially perceived as catastrophic and appeared to be influenced more by wind speed and direction than by subtle patterns in fuels and topography.

Fire managers and ecologists have found it challenging to determine the relative importance of fuels or weather on fire behavior. Fuel differences among stands appear to be more important in fires that occur during less extreme weather conditions, thus burning smaller areas, but weather may be the key driver under the more extreme weather conditions in which the largest areas typically are burned (Bessie and Johnson 1995). A forest stand consists of many layers of surface, ladder, and crown fuels, and we expected that stands of higher density would burn more severely and experience higher tree mortality. The influence of topography on fire behavior may also be greater on steep slopes, ridgetops, and south and west aspects, and we expected that these areas would burn more severely. Topography influences the distribution of vegetative communities with varying flammabilities, and steep slopes permit preheating and ignition for a fire burning uphill (DeBano et al. 1998). In general, fires that occur in low and moderate weather conditions result in small surface fires with sporadic crowning, while fires occurring in extreme weather conditions often become large crown fires (Bessie and Johnson 1995). We expected that weather strongly influenced burn severity due to the extensive area burned by the Jasper fire. We also expected that days with high wind speeds and temperatures would have a higher proportion of area burned by high severity. Days with higher proportions of high- severity fire might also be larger in size. Investigation of the complex interaction of weather, fuels, and topography may help to identify conditions or thresholds that lend themselves to fire behaviors that can be addressed by management and those that cannot.

METHODS

2.1 Study Area

The Black Hills is an isolated and forested mountain range rising over 1000m above the Great Plains in western South Dakota and northeastern Wyoming (Shepperd and Battaglia 2002). As the easternmost extension of the Rocky Mountains, the Black

Hills was formed by regional uplift ~ 35 to 65 million years ago. This uplift produced an elliptical dome with an older crystalline core surrounded by younger, steeply dipping sedimentary deposits (Froiland 1990). The Limestone Plateau surrounds the core and the area burned by the Jasper Fire is located on the southwestern extent of this plateau (Fig. 1). In the study area, latitudes range from 43° 41' 35" to 43° 55' 48" and longitudes range from 103° 46' 1" to 104° 0' 47". The mean daily maximum and minimum temperatures are -3.3 and 13.2 °C, and annual precipitation ranges from ~ 45 to 48 cm. Sixty-five to 75 % of precipitation, commonly in the form of intense thunderstorms accompanied by lightning, coincides with the growing season (Froiland 1990). Good seed years are common, and natural regeneration is prolific in the study area and throughout the Black Hills.

2.2 Development of burn severity layer

A burn severity map was produced in 2001 from 30- meter resolution LANDSAT 7 imagery taken one year after the fire (Gould 2003). An unsupervised classification produced ten classes of similar pixels. Gould (2003) surveyed three randomly selected sites within each pixel class to calibrate and improve the classification process. At each site, information was collected about ground surface and subsurface conditions. For each pixel class, the proportion of the area occupied by rock, bare soil, duff, litter, and vegetation was calculated. Pixel classes exhibiting similar characteristics of unprotected soil (vegetation and duff) and unprotected (rock, bare mineral soil and litter without duff) were grouped into low, moderate, and high burn severity classes (Table 1). We validated the burn severity imagery by repeating the previously described survey at 10 randomly selected sites within each burn severity class. We correctly classified burn severity ~ 70 % of the time.

We used the Patch Analyst© extension in ArcView GIS® to examine spatial patterns of burn severity at the landscape level. We created patches by dissolving boundaries between adjacent polygons of the same burn severity. Class and landscape metrics include number of patches, mean patch size, patch size standard error, median patch size, area -weighted mean shape index (AWMSI), mean patch edge, patch edge standard error, mean core area, and core area standard error (Elkie 1999). We determined patch edge from the perimeter of each patch. Within high severity patches, we identified core areas that were potentially vulnerable to cover type conversion due to seed dispersal limitations. We used 30 m as an estimate of maximum effective seed dispersal distance since ponderosa pine seeds disperse within ~ 1 to 1.5 times parent tree height (Boldt and Van Deusen 1974; Shepperd and Battaglia 2002).

We compared size and edge distributions for patches of different burn severity with a nonparametric multi-response permutation test (Mielke and Berry 2001). Multiple comparisons for the multi-response permutation tests were based on Peritz closure (Petrondas and Gabriel 1983) and tested for significance at the 95 % confidence level (alpha = 0.05).

Daily fire spread maps (JRAT 2000) (Fig. 2) were used to explore the influence of weather conditions on burn severity. Daily fire size reflects the suite of burning conditions (wind speed, wind direction, fuel moisture) that influence fire behavior (Turner et al. 1994). We obtained hourly weather conditions for Custer, SD (Lat 43°44'N Long 103°22'W), from the National Climatic Data Center website (http://www.ncdc.noaa.gov/oa/ncdc.html). We calculated hourly fuel moisture conditions during active fire days using the Remsoft Behave program (Bradshaw 1983; Cohen 1985). Hourly weather and fuel moisture conditions were summarized for active burning periods (10am to 6 pm) represented by daily fire spread maps. First, we used a stepwise regression analysis (SAS Institute 2001) to explore relationships between total area burned per day and the following weather- related variables: 1, 10, 100, and 1000-hour time-lag fuel moisture (TLFM); mean relative humidity; maximum temperature; minimum temperature; wind speed, and wind gust speed. Secondly, we used stepwise multiple regression to examine the relationship between the proportion of total daily burned area in each burn severity class and the same weather and fuel moisture variables listed above. Lastly, we used regression analysis to determine the strength of the relationship between the proportion of total daily burned area in each burn severity class and the total area burned each day.

A general description of the area burned by the Jasper fire was developed using ArcView GIS 3.2® and SAS V8.0. Pre-fire stand condition and structural information was obtained from the 2000 Resource Information System (RIS) database. Topographical information including elevation, slope, and aspect was gathered from the 30m resolution Digital Elevation Model (DEM) for the Black Hills. The RIS and DEM layers were combined with the burn severity layer to produce a GIS layer containing topographical, pre-fire structural, and burn severity attributes. Information relating to trees ha^{-1} in size classes > 13 cm and < 13 cm, average stand diameter (ASD), crown cover, stand basal area (BA), and stand density index (SDI) was extracted from the RIS database. SDI is a relative measure of stand density that provides a relationship between stand basal area, trees per unit area, average stand diameter, and stocking of a forested stand. SDI converts a stand's current density into a density at reference size. Relative density compares the density of a stand relative to some biological limit, and maximum stand density index varies by species (Reineke 1933).

We randomly selected 500 points from each burn severity class within the ponderosa pine cover type to determine the strength of the relationship between burn severity and topography and forest structure. We performed all summary and statistical analyses in SAS V.8.0. Variables were tested for significance at the 95% confidence level (alpha = 0.05) in an ANOVA model (PROC GLM, SAS Institute 2001).

A non-parametric model was then applied to the same data set to explore relationships between burn severity and topography and structure. We used S-PLUS® v. 6.2 (2000) to construct a decision-tree regression analysis (Breiman et al. 1984) in which an overall accuracy of classification was assigned to each burn severity within the model. The model creates a tree structure from the data in which each branch is split into mutually exclusive subsets. Each branch of the tree corresponds to a rule for splitting the data into subsets that yield predictions of low, moderate, or high burn severity given the values of the dependent variables.

RESULTS

The Jasper fire area is characterized by gentle topography and relatively minor elevational change. We found ~ 3 % of the Jasper fire area was > 40 % slope. Elevations range from ~1500-2100 m.

The USDA Forest Service Black Hills National Forest manages 95 % of the area burned by the Jasper Fire. Interior ponderosa pine stands in various successional stages formed the dominant vegetation matrix, but scattered aspen (*Populus tremloides*) clones and meadowland inclusions were found in the study area. Aspen clones were found on ~ 1 % of the area and grasslands occur on ~ 7 % of the burned area.

Pre-fire stands were relatively homogenous with high continuity in surface and canopy fuels. Well-stocked ponderosa pine stands were found on 87 % of the burned area. Stands were occupied by saplings, mature pole- sized trees, and small sawtimber. Pre-fire ASD was 25.0 cm. Before the Jasper fire, 61% of ponderosa pine forests were in a mature Habitat Structural Stage (HSS) (4A, 4B, and 4C). These forests had moderate to high canopy cover, and 29 % of forests had canopy cover > 70 %. On average, there were 388 trees ha^{-1} > 13 cm and 1538 trees ha^{-1} < 13 cm DBH (diameter at breast height). For all stands in the study area, average basal area was 18 m^2ha^{-1}. Average SDI was 145 or ~ 32% of maximum stand density. Relative density compares the density of a stand relative to the biological limit of 450 for Black Hills ponderosa pine. Mean site index for ponderosa pine stands within the burned area was 58 (base age = 100 yrs) (Table 2).

In spite of subtle topography and homogeneity of vegetation structure and composition, the Jasper fire was large, and the burn mosaic was complex. For the entire Jasper fire area, we documented a patchy mosaic where 25 % of the landscape burned in low severity, 48 % in moderate, and 27 % in high severity (Fig. 3). In the ponderosa pine cover type, 18, 53, and 29 % burned in low, moderate, and high severity. Most grasslands and aspen clones burned in low severity when compared to conifer-dominated areas. We found 87, 10, and 3 % of grasslands burned in low, moderate, and high severity. In aspen stands, we found 55, 24, and 21 % burned in low, moderate, and high severity.

Patch size was significantly different in low, moderate, and high severity ($P < 0.0001$). Patch size averaged 10, 24, and 8 ha for low, moderate, and high burn severity, and largest patches were up to 1550, 3475, and 900 ha. Median patch sizes were 2, 2 and 1 ha in low, moderate, and high severity (Table 3). Roughly ~ 55 % of the area burned in low and moderate severity was found in patches > 250 ha in size (Fig. 4). Two patches, each ~ 1000 ha in size represented ~ 30 % of the total area burned in low severity. Two patches, each ~ 3000 ha in size, represented ~ 40 % of the total area burned in moderate severity. Approximately 60 % of the area burned in high severity was found in patches < 50 ha in size (Fig. 4). We found 15 % of individual high severity patches were < 1 ha in size. A single large ~ 900 ha patch represented ~ 10 % of the total area burned in high severity.

The amount of edge in patches of low, moderate, and high severity was significantly different ($P < 0.0001$). Patches of low and moderate severity were more complex in shape creating a greater amount of edge compared to high severity patches. High burn severity resulted in relatively small, more circular patches with less edge. The average core area in high severity patches was ~ 2 ha (Table 3). Fifty-five percent of the area that burned in high severity was within 30 m of a potential tree seed source in adjacent low or moderate severity patches. We found ~ 99 % of the area that burned in high severity was within 200 m of a live edge. Forty-five percent of the area in high severity was outside the effective seed dispersal distance for ponderosa pine and represented 12 % of the total burned landscape

Despite the heterogeneous landscape imprint of burn severities, mixed severity burning in the Jasper fire was not primarily weather dependent. Weather conditions remained very hot and dry throughout the Jasper fire (Table 4), fuel moisture conditions were at record low levels (Table 5), and atmospheric conditions were very unstable. These conditions resulted in extreme fire behavior; however, we found little variation in fuel moisture and weather conditions from day to day, except on the third day when a large crowning run sustained by high wind speeds and gusting pushed spread rates to ~40 ha $\min^{-1}$. Even under the range of extreme burning conditions, the proportion of burn severity that occurred from day to day was stable, suggesting that mixed mode burning was constant at very severe fuel moisture and weather conditions. We found no statistically significant relationships ($P < 0.05$) between the proportion of total daily burned area in each burn severity class or daily fire size and fuel moisture and weather conditions. We found no statistically significant relationships between total daily fire size and proportion of low, moderate, and high severity within daily burned areas. Thus, weather and fuel moisture conditions were not strong predictors of burn severity in our dataset, and we chose to omit this information in subsequent models.

In contrast, we found that the proportion of the Jasper fire that burned at low, moderate, and high severity was related to vegetation structure and topography. SDI, slope, the number of trees > 13 cm DBH, and the number of trees < 13 cm DBH, ranked in order of importance, are significant predictors of burn severity ($P < 0.05$). ASD, aspect, percent crown cover, and elevation, ranked in order of least importance, were not significantly different in areas of different burn severity (Table 5).

Stand density index was the most important variable in predicting burn severity (Fig. 5). At SDI's < 185 or relative densities < 40 %, we correctly classified burn severity as either low or moderate 78 % of the time. Eighty-five percent of all the observations of low or moderate severity occurred at low relative density. In stands with lower relative density, we incorrectly classified high severity 22% of the time which accounted for 47% of high severity observations. Conversely, when relative density exceeded 40%, we correctly classified high burn severity 63% of the time. Fifty-three percent of all the observations of high severity occurred at high relative density. We incorrectly classified low or moderate severity 37 % of the time which accounted for only 15% of low or moderate observations.

The second most important variable in the model was either the number or size of trees (Fig. 5). When relative density was high and there were fewer than ~230 trees > 13 cm ha^{-1}, we correctly classified low and moderate severity 83% of the time. Lower relative density and fewer large trees accounted for ~55% of low and moderate observations. When relative density was not high and a greater number of larger trees were present (trees $ha^{-1} > 230$), slope entered the model. At slopes < 18%, we correctly classified low and moderate severity 76% of the time. When there were fewer small trees (DBH < 5 cm), we were more likely to observe low than moderate severity fire. This classification related to ~ 20 % of low and moderate observations. Conversely, at slopes > 18 %, we correctly classified high severity 42% of the time which accounted for 11% of observations of high severity. If relative density exceeded 40%, then average stand diameter entered the model. When average stand diameter was < 24 cm and slope > 25 %, we correctly classified high severity 53 % of the time. This scenario of high relative density within a stand of smaller trees on steep slopes accounted for ~ 25 % of all high severity observations. When slopes were < 25 %, we were more likely to observe moderate than high- severity fire. In stands of higher relative density with larger trees

(ASD > 24 cm), high burn severity was correctly classified 80% of the time. Again this scenario accounted for ~ 25 % of all high severity observations.

Model classification accuracy was high, and we were able to correctly classify burn severity based on information relating to SDI, the proportion of the stand composed of trees in various sizes classes, the average stand diameter, and slope ~71% of time (Table 7).

DISCUSSION

Despite extreme weather conditions, fire behavior in the Jasper fire was modified by subtle differences in forest structure and landscape position. This observation was surprising because most of the area burned by the Jasper fire contained mature, moderate to high density, second growth ponderosa pine. The homogeneity of forest structure and vegetation composition, in concert with extremely low fuel moistures and high winds created ideal conditions for a running crown fire with high spread potential. Although ~ 60 % of the area burned in < 12 hours, fire effects were heterogeneous, and we found many small patches of low, moderate, and high burn severity in roughly equal proportion on the landscape. While heterogeneous effects have been documented following other large wildfires, (Lyon and Stickney 1974; Whelan 1995; DeBano et al 1998; Turner et al. 1994; Turner and Romme 1994; Turner et al. 1997; Turner et al. 1998; Graham 2003; USDA 2002, 2003), the landscape imprint of the Jasper fire was distinctly different. The Jasper fire was not dominated by high severity components, nor fatal to most forest vegetation. This was in spite of the fact that the Jasper fire occurred under drought conditions on one of the most intensively managed national forests in the west, subjected to over a century of fire suppression.

We found a complex mosaic of burn severities and unburned areas on the landscape following a fire event that appeared to have been strongly influenced by extreme weather conditions. The summer had been extremely dry, and when the fire started, daytime relative humidities were ~ 15 %. Fuel moisture levels of 10- hour fuels were ~ 60 % lower and 100 and 1000- hour fuels were 18- 26 % lower than the 10 year average (1991-2002) (Benson and Murphy 2003). Very strong and gusting winds caused the Jasper fire to grow from ~ 3500 ha to nearly 20,000 ha in one day, creating firestorm conditions, and raining ash on urban areas ~ 50 km to the east (JRAT 2000).

Several interesting contrasts and similarities exist between the Jasper fire and the 2002 Hayman fire in Colorado's Front Range. Prolonged drought conditions led to abnormally low fuel moisture contents (5- 10 %) of woody fuels of all sizes in the Hayman fire area. During the Hayman fire, high winds (20 to 50 mph), gusts to 84 mph, and low humidity (~ 10 %) resulted in extensive runs and widespread crown fire with long-range spotting (Graham 2003). The Haines Index was 6, the highest level of atmospheric instability, on the day when each fire experienced large crowning runs (JRAT 2000; Graham 2003). Extreme fuel and weather conditions and steep terrain combined to severely burn ~ 28,000 ha, roughly half of the landscape burned by the Hayman fire, within a 24-hr period (Graham 2003). However, in the Jasper fire even when daily fire size was large, we observed a relatively even distribution of burn severities.

While the overall proportion of the Jasper fire that burned at a given severity was most likely related to extreme weather conditions, the variation in the proportion of burn severity during a day was not caused by weather. We found no statistically significant relationships between daily burned area or the proportion of each burn severity class represented on a daily basis and fuel moisture and weather conditions. Following the 1988 Yellowstone fires, Turner et al. (1994) found that nearly half the variance in daily burned area was explained by 100- and 1000- hour fuel moistures and relative humidity. One, 10, and 100-hour TLFM; maximum temperature; and minimum relative humidity significantly influenced the proportion of each burn severity class represented on a daily basis (Turner et al. 1994); however, the Yellowstone fires were much larger and burned over several months in a landscape that was historically less frequently and more severely burned.

Many of the variations in effects and response to fire result from variation in burn severity and patch size (Pickett and White 1985). Patch sizes in the Jasper fire were small relative to daily area burned, and the largest patches in low and moderate severity burned over multiple days. High- severity fire burned > 9,000 ha (27 %) during the Jasper fire; however, the proportion of area burned by high- severity fire was stable from day to day. The largest high severity patch burned in a few hours, but was much smaller than the largest burned patches in low and moderate severity. Large burns tended to have a greater percentage of crown fire and smaller percentages of light surface burns in the Yellowstone fires (Turner et al. 1994). Crown fire burned 31 % or ~ 70,000 ha in subalpine lodgepole pine (*Pinus contorta* var. *latifolia*) forests in the Yellowstone fires, and large patches of crown fire were 500- 3600 ha (Turner et al. 1997). In the Hayman fire, 33 % of the area was classified as high severity, and the largest patch of complete mortality was ~ 3500 ha (Graham 2003). Small "escapes" or narrow "tree crown streets" were embedded within large patches of crown fire in these montane ponderosa pine

(*Pinus ponderosa* var. *laws*) and Douglas- fir (*Pseudotsuga menzensii*) forests. The proportion and patch sizes of high- severity fire were much smaller in Jasper; and rather than patches of surviving vegetation within a matrix of crown fire, a matrix of surviving vegetation was interspersed with patches of crown fire on the Jasper landscape.

The spatial mosaic of burn severities exerts a strong influence on vegetation recovery following high- severity fires. Extensive areas of high- severity fire may have fewer resprouting individuals or surviving trees to provide seeds (Turner et al. 1994; Graham 2003). Unburned or lightly burned patches within severely burned areas may provide seed sources to increase rates of plant recovery. In the Yellowstone fires, smaller patches were often more heterogeneous in fire effects and overall less severely burned, whereas larger patches were more homogenous in effects and more severely burned (Turner et al. 1994). Five years post- fire, the Yellowstone landscape was characterized by extensive lodgepole pine regeneration in large, open patches, although forest reestablishment was limited in areas of low prefire serotiny (Turner et al. 1997). The extent of patches of high burn severity had not occurred within the Cheesman landscape, located near the center of the Hayman burn, in the past 700 years according to reconstructions of fire history and forest dynamics. A rapid return to prefire condition is expected in areas that burned at low severity in the Hayman fire; however, large openings may persist without significant tree cover for a long time due to lack of seed source (Graham 2003).

In contrast to other large fires, we found large patches were often more heterogeneous in fire effects and less severely or moderately burned following the Jasper fire. Low and moderate severity patches averaged ~ 10 and 24 ha in size and were within

10 m of a green edge. High severity patches were small, averaging ~ 8 ha in size, and over half of the area that burned in high severity was within the effective seed dispersal (30m) of a surviving ponderosa pine in adjacent low or moderate severity patches. In Yellowstone, 25% of the area burned by crown fire was > 200 m from unburned or lightly burned areas (Turner et al.1994). In Jasper, 99% of the area that burned under high severity was within 200 m of a green edge. The juxtaposition of low, moderate, and high severity patches in the Jasper fire created a mosaic effect with clumps of forests of variable density mixed with smaller severely burned areas.

There was a significant effect of stand structure and topography on burn severity under the severe weather conditions during the Jasper fire. Mean relative density in the study area was ~ 30 % before the fire, approaching full site occupancy for Black Hills ponderosa pine. Relative density, the number of large trees, and slope were the most influential variables in determining low and moderate burn severity. Low numbers of large trees on gentle slopes resulted in the most likely scenario for low or moderate burn severity. Stands with lower density (RD < 40 %) comprised of a smaller number of large trees (trees $ha^{-1} < 230$) were not highly likely to burn in high severity.

Forest stands with widely- spaced crowns generally support a faster spreading surface fire than those with dense crowns (Debano et al. 1998). Harrington (1982) documented low crown fire risk, and high rates of fire spread and high fire intensities in mature groups of ponderosa pine (*Pinus ponderosa* var. *arizonica*). The open nature of mature stands fostered a warm, dry environment where fine fuel moistures were low and ignition potential of surface fuels was high. The accumulation of litter and absence of large woody fuels provides a possible explanation for less severe fire effects in open, mature stands (Harrington 1982). In less dense stands, we found tree size was important in predicting burn severity at steeper slopes. Slopes can influence fire similarly to the effects of wind by pushing flames to the ground surface and pre-heating fuels ahead of the flame front or by increasing rates of spread (Debano et al. 1998). Stands with lower density comprised of a greater number of large trees (trees $ha^{-1} > 230$) were not highly likely to burn in high severity when slopes were < 18 %. However, at steeper slopes, the crowns of large trees are effectively stacked in a multi-layered arrangement that facilitates fire spread from crown to crown.

The spatial continuity and density of tree canopies combine with fuel moisture and wind to determine rate of fire spread and severity (Rothermel 1983, 1991). Graham et al. (2004) reported that the potential for crown fires was high in many western forests with homogeneous and continuous horizontal and vertical stand structures. We found high stand density presented the most likely scenario for crown or high- severity fire. Stands with high density (RD > 40 %) consisting of larger trees (ASD > 24 cm) or many small trees were likely to burn in high severity. When the continuity of surface fuels to crown fuels was high, then crown fire ignition was more likely. Stands with many small trees tended to have low crown base heights and to create fuel ladders. In contrast, branches of larger trees in dense stands self-prune, raising crown base height. The potential for surface fire to transition to crown fire is decreased in stands with higher crown base height that have less vertical continuity between surface and canopy fuels (Van Wagner 1977). However, there is high potential for fire to pass from crown to crown in dense stands. Canopy bulk density is the foliage contained per unit volume of a forest stand (Scott and Reinhardt 2001) and effectively represents crown fire hazard

(Peterson et al. 2003). High burn severity was probably more predictable in dense stands with large trees due to high canopy bulk density, while the horizontal patchiness of less dense stands likely reduced the spread of fire within the canopy stratum.

The imprint of mixed- severity fire over extensive spatial and temporal scales results in a coarse- grained landscape mosaic characterized by fine-grained patches with varying proportions of surviving trees and fire-killed trees, some young, even-aged forest patches, and some small openings. Because stands with different structural characteristics are contiguous on the landscape, a fire starting in a stand more likely to burn less severely will eventually reach a stand likely to burn at higher severity. Dense stands with many small trees create ladder fuels and facilitate fire growth when fire reaches larger trees. Black Hills forests are dense with high canopy cover, and these conditions increase the probability of surface fires developing into crown fires. Fine surface fuels associated with productive overstories and vertical ladder fuels in the form of dense regeneration and understory thickets with a high degree of continuity are common on the Black Hills landscape. In these managed, relatively homogenous forests, basic elements of forest structure favored mixed- mode burning. We believe that the patterns of burning that we observed following the Jasper fire may characterize typical behavior for infrequent, large fires in the Black Hills. While it is difficult to distinguish between conditions that tend to burn in low and moderate severity, it is relatively easy to identify thresholds of forest structure where crown fire is likely to occur. Weather conditions more extreme than observed during the Jasper fire are rare, yet we still found many small patches of low, moderate, and high severity. Our conclusion that structure does influence burn severity has important implications in terms of fuels management and in understanding patterns of vegetation that influence burn severity even in events occurring during extreme weather conditions.

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Figure 2.5. Partial classification tree for burn severity predicted by stand density, tree size, and slope.

Table 2.1. Description of visual impacts to soil and vegetation in areas of different burn severity.

Burn Severity	Fire Type	Fire Effects
Low	Surface	Limited canopy effects; low tree mortality; most duff and litter retained with dense revegetation observed; > 70 % of forest floor covered with vegetation, duff, and/or litter
Moderate	Mixed surface & crown	Greater canopy effects and some tree mortality; vegetation and duff retained in patches; soil covered with scorched needles; 50-70 % of forest floor covered with vegetation, duff, and/or litter
High	Crown	Aboveground vegetation, litter, duff, and needles in canopy mostly consumed; extensive tree mortality; limited revegetation; > 50 % of overall area composed of rock, bare mineral soil, and/or litter with no remaining duff

Table 2.2. Description of pre-fire stand characteristics within study sites in the Jasper fire (n = 1500). [1]

Average Stand Diameter (SE) (cm)	Density (SE) (trees ha^{-1} > 13 cm)	Density (SE) (trees ha^{-1} < 13 cm)	Basal Area (SE) (m^{2}ha^{-1})	Stand Density Index	Relative Density (%)	Site Index (base age= 100)
25.3 (1.9)	388.3 (86.9)	1538.1 (799.7)	17.7 (3.1)	145 (82)	32.2 (18.2)	58 (10)

[1] **Data summarized from 2000 Resource Information System database for the BHNF.**

Table 2.3. Distribution, number, size (SE), and shape of patches in burn severity classes in the Jasper fire. [1]

Burn Severity	% of land-scape	# of patches	Mean Patch Size (SE) (ha)	Median Patch Size (ha)	Shape Complex-ity (AWMSI)	Mean Patch Edge (SE) (m)	Mean Core Area (SE) (ha)
Low	25	824	10.4 (2.7)	2.2	10.6	2254.3 (498.2)	0.8 (2.0)
Mod-erate	48	674	24.1 (7.1)	2.0	13.2	4448.5 (1051.9)	4.8 (18.2)
High	27	1201	7.5 (1.0)	1.3	3.9	1769.5 (113.3)	2.4 (9.2)
Land-scape	100	2699	12.5 (2.0)	1.8	10.1	2586.5 (308.3)	2.4 (11.0)
Pr > F			< 0.0001 **			< 0.0001 **	

[1] **Data summarized from burn severity map (Gould et al. 2003)**

** **(P < 0.0001 denotes significance)**

Table 2.4. Summary of fire size, proportion burned within each severity class, and weather conditions (10am to 6 pm) for the eight days of active burning during the Jasper fire.[1]

Date	Daily Fire Size (ha)	Proportion of Daily Area Burned by Severity Class			Wind Speed (knots)	Wind Gusts (knots)	Min. Daily Temp °C	Max. Daily Temp °C	% RH[2]
		% Low	% Moderate	% High					
8/24	1479	14	59	28	8	17	16	32	16
8/25	3414	17	49	33	5	0	13	27	38
8/26	19768	27	45	27	11	19	11	31	24
8/27	1707	21	64	15	6	0	13	27	32
8/28	1925	15	59	26	9	18	10	24	40
8/29	2986	34	51	15	8	13	9	27	35
8/30	2133	24	37	39	9	18	11	28	30
8/31	348	43	38	19	11	17	9	17	58

[1] Data summarized from National Climatic Data Center database for Custer, SD

[2] Relative Humidity

Table 2.5. Summary of fuel moisture conditions (10am to 6pm) and the Haines Index for the eight days of active burning during the Jasper fire.[1]

Date	1-hr TLFM[2]	10-hr TLFM	100-hr TLFM	1000-hr TLFM	Haines Index
8/24	2.6	3.2	4.2	5.2	6
8/25	6.1	7.6	8.6	9.6	6
8/26	4.3	5.3	6.3	7.3	4
8/27	5.6	7.0	8.0	9.0	5
8/28	6.6	8.2	9.2	10.2	5
8/29	5.2	6.5	7.5	8.5	5
8/30	4.4	5.5	6.5	7.5	5
8/31	8.8	10.9	11.9	12.9	4

[1] **Data summarized from National Climatic Data Center database for Custer, SD and Remsoft Behave program (Bradshaw 1983; Cohen 1985).**

[2] **Time-lag fuel moisture**

Table 2.6. Regression of standard site conditions with burn severity.

Independent Variables	General Linear Model Pr > F
Average Stand Diameter	0.5826
% Crown Cover	0.1659
TPA > 13 cm	< 0.0001 **
TPA < 13 cm	0.0445 **
Stand Density Index	< 0.0001 **
Elevation	0.0725
Slope	< 0.0001 **
Aspect	0.4524

** **(P<0.05 denotes significance)**

Table 2.7. Model accuracy for classification of burn severity.

Burn severity	Model Accuracy (%)
Low	74
Moderate	64
High	76
Overall	71

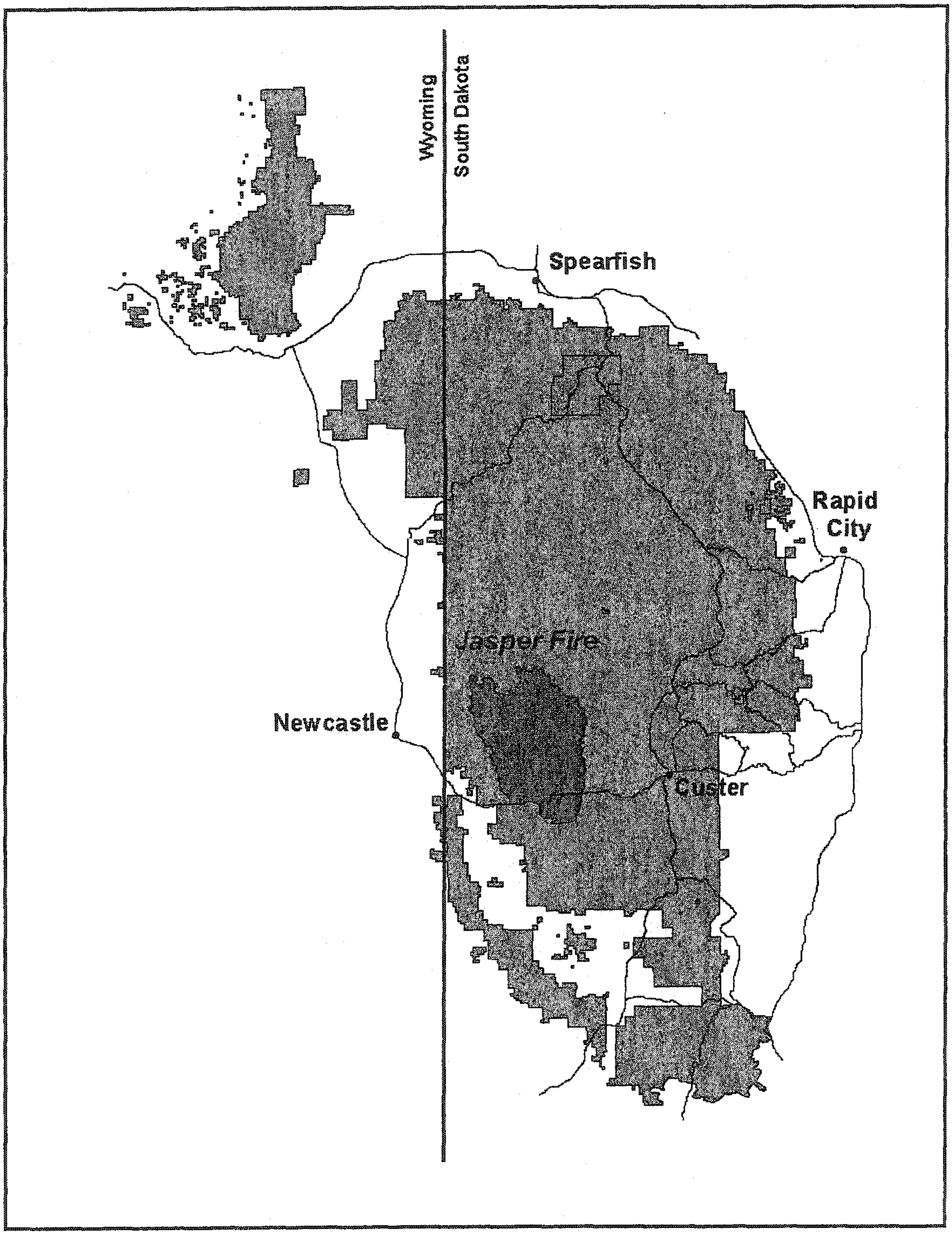

Figure 2.1. Location of Jasper fire in western South Dakota on the Black Hills National Forest.

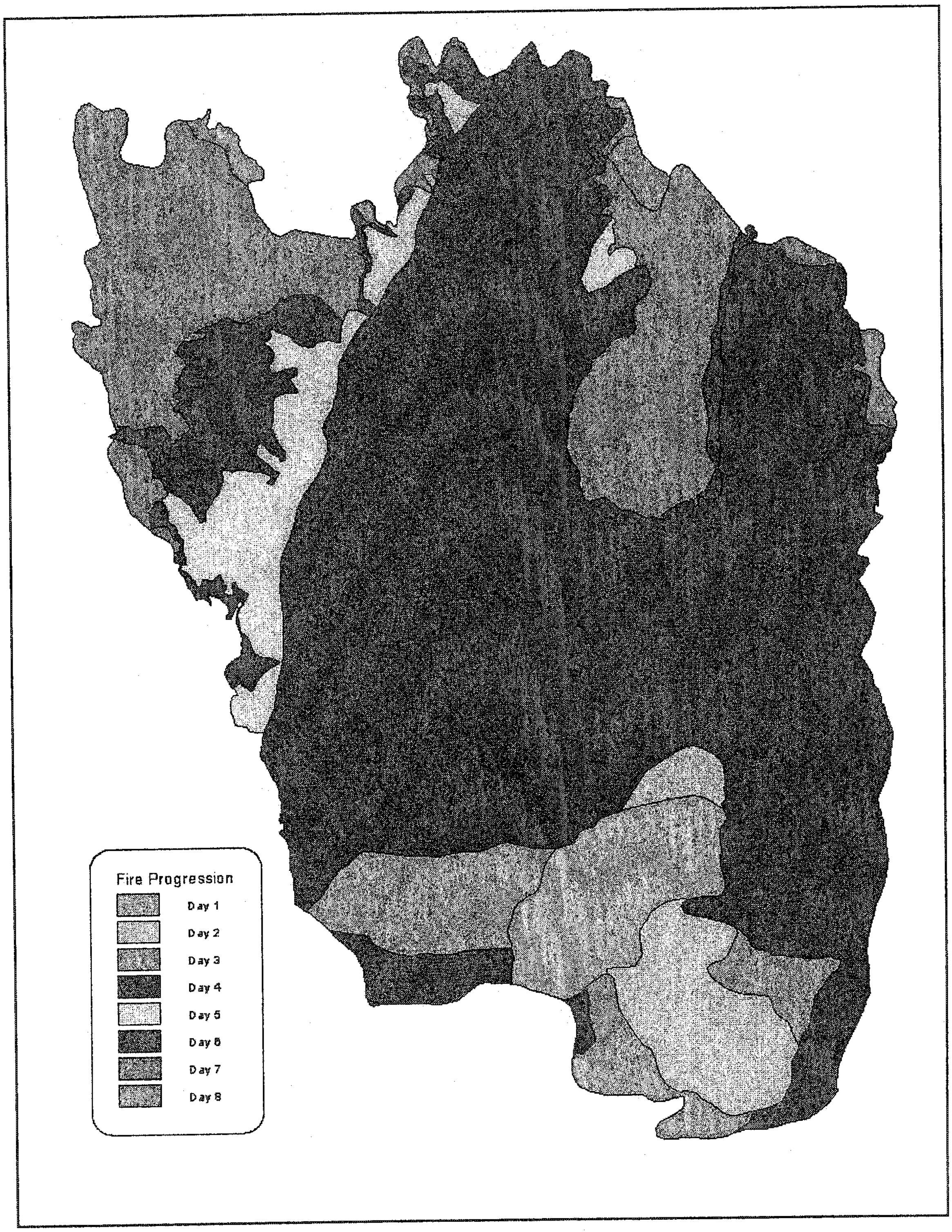

Figure 2.2. The Jasper fire progression map.

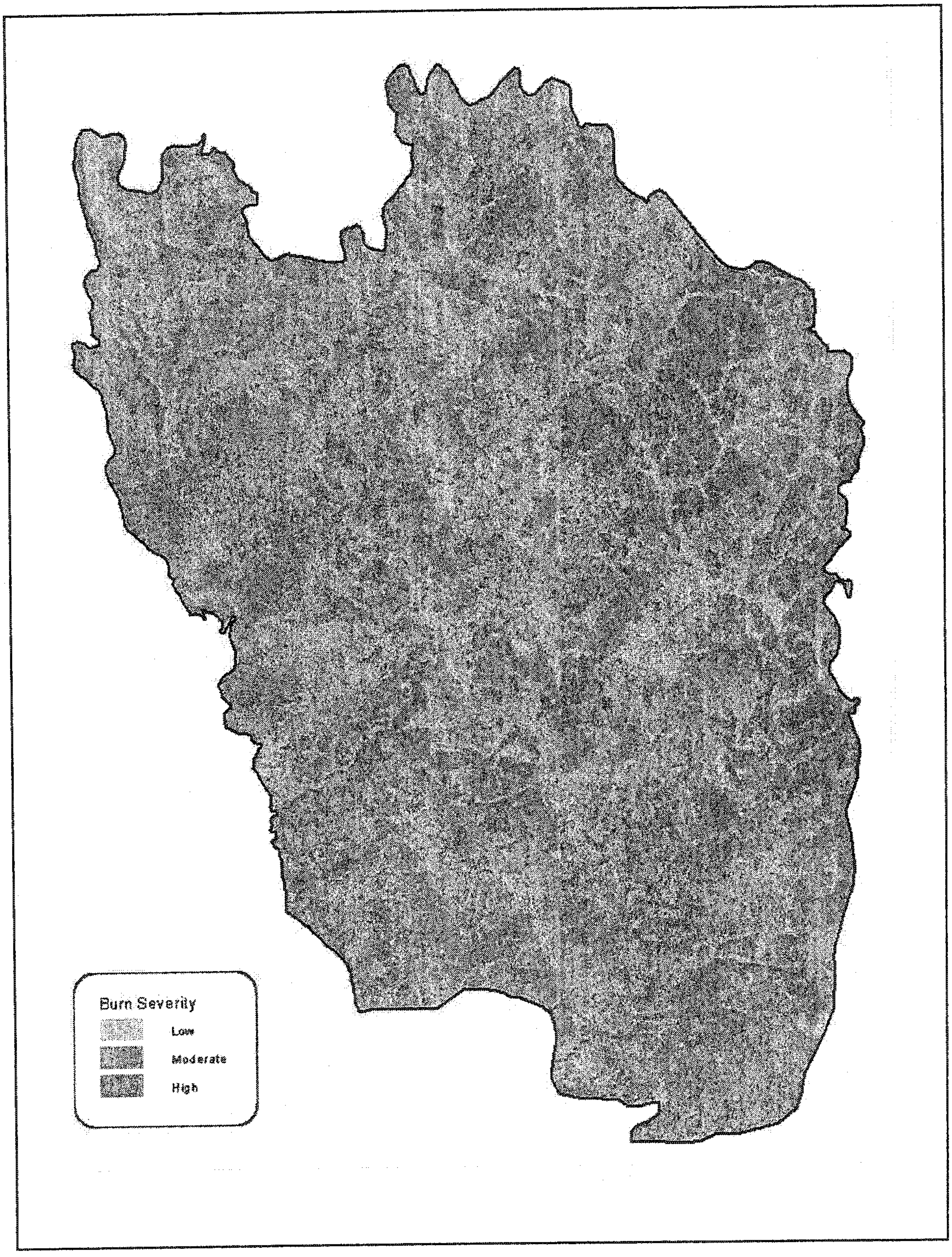

Figure 2.3. Burn severity map for the Jasper fire.

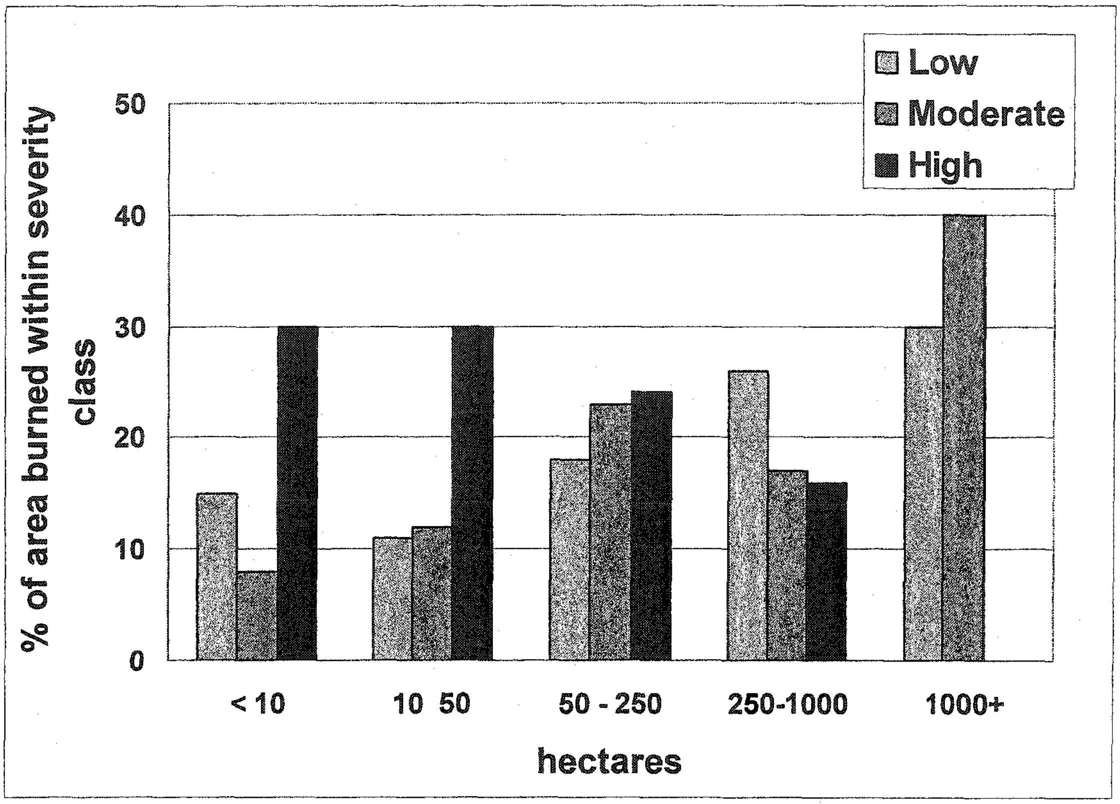

Figure 2.4. Distribution of low, moderate, and high severity patches.

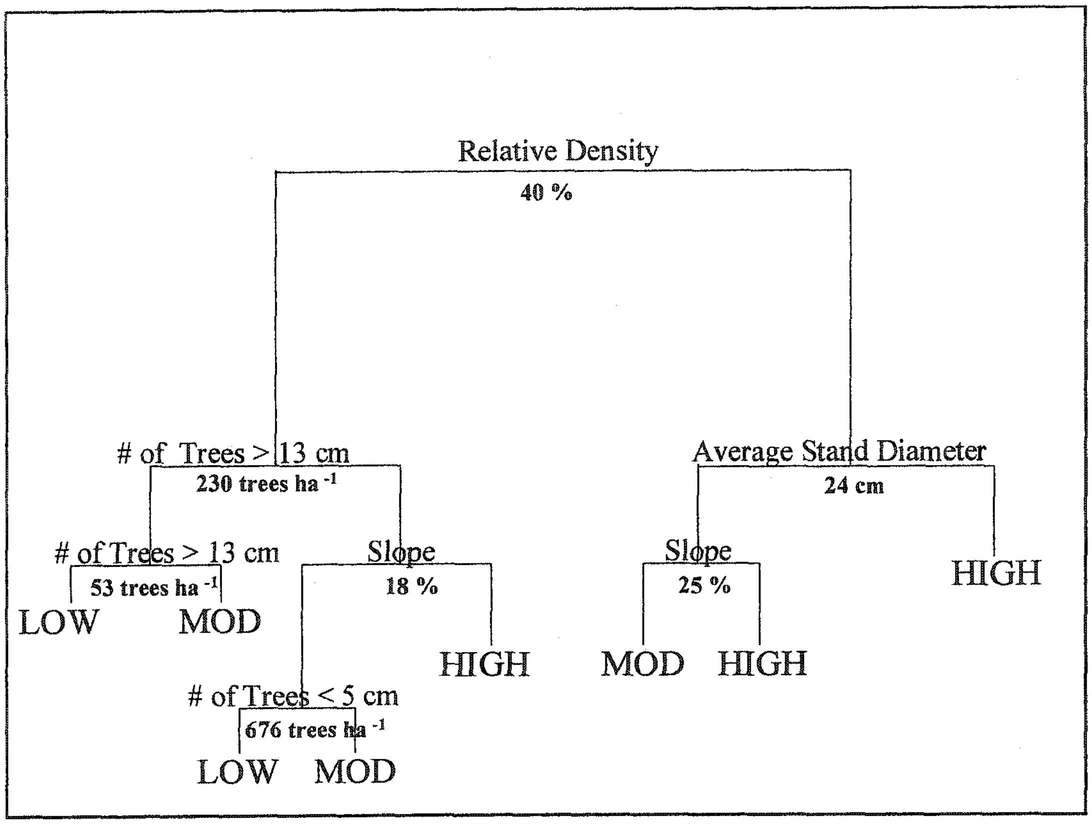

Figure 2.5. Partial classification tree for burn severity predicted by stand density, tree size, and slope. Values greater than the cutoff classify to the right, lesser values classify to the left.

III. EFFECTS OF MIXED- SEVERITY FIRE ON VEGETATION AND SOILS IN BLACK HILLS PONDEROSA PINE FORESTS

ABSTRACT

The 2000 Jasper fire burned ~33,000 ha in Black Hills ponderosa pine forests, creating a mosaic of fire effects in patches of low, moderate, and high severity. This mixed- severity fire left a landscape imprint distinct from other recent, large, western wildfires. Rather than small patches of surviving vegetation in a matrix of crown fire, we observed small patches of crown fire interspersed among large patches of surviving vegetation. We inferred variable fire effects on aspects of canopy, understory plant communities, forest floor, soil and differential rates of recovery to be the result of different burn severity. Tree mortality increased from ~1 to 16 % and 18 to 59 % in low and moderate severity patches during the first three years post-fire. All trees were killed in high severity patches. Greater reductions in plant cover were seen with greater severity. Herbaceous cover and richness recovered to pre-burned levels in all burned areas within three years post-fire. Fire initially removed aboveground shrub components, independent of severity, although shrub cover recovered to ~ 40 % of pre-burn cover in high severity areas three years post-fire. Pre-fire species composition was highly influential in determining post-fire species composition, and we found ~ 70 % of species regenerated vegetatively. We found three times more non-native plant species following fire. Soil nitrogen availability was 21 to 41 times greater in areas of low and high severity than in unburned areas, but decreased two years post-fire. Tree regeneration was limited and variable in the first three years post-fire. Many small patches of low, moderate, and high burn severity with a high proportion of surviving vegetation accelerated rates of recovery in the Jasper fire compared with other recent and large western fires.

INTRODUCTION

Ecologists have long recognized the enormous variability in fire effects and vegetation response that results from even the most severe fires (Turner et al. 1994; Turner and Romme 1994; Turner et al. 1997; Peterson 1998). Causal factors, fire effects and ecosystem response to fire vary over time and space within dynamic systems and defy simple classification. Fire effects on soil and vegetation and rates of resource recovery may vary according to burn severity (Ryan and Noste 1985; Turner and Romme 1994; DeBano et al. 1998), and burn severity is largely driven by the dynamic interaction of fire behavior and fuels (Debano et al. 1998). For this reason, the concept of severity has been used to characterize fire regimes as low, high, and mixed. Mixed- severity fire regimes have been least described perhaps due to the complexity inherent in the study of variable severity at multiple temporal and spatial scales (Brown and Smith 2000). Mixed- severity fire regimes may be the result of fine-scale, topographically-influenced differences in vegetation and fuel moisture that cause low- and high- severity fires to burn in proximity, although this transition is poorly understood (Fulé et al. 2003). Severity may also vary within a single fire depending on complex interactions of weather, vegetation, and topography (Rowe and Scotter 1973; Wright and Heinselman 1973; Lyon and Stickney 1974; Van Wagner 1983; Turner et al. 1994) and produce a wide range of local effects on vegetation, forest floor, and soil resources. The additive effect of temporally- explicit fires where surface, crown, and a combination of these fire types produce a fine-grained pattern of stand structure and fuels may also be described by mixed- severity fire regimes. Irregular burning patterns characterize mixed- severity fire regimes, and past burn mosaics increase the likelihood that future mixed burning patterns will occur (Brown and Smith 2000). Because large-scale, mixed- severity fires are heterogeneous in their effects across the landscape, such events provide ideal opportunities for investigating the influence of burn severity on post-fire ecological processes within a little studied fire regime.

Mixed- severity fire regimes in the Black Hills have described large, severe fires that occurred at longer intervals within interior forests and less severe, surface fires that burned more frequently in the ecotone between forest and prairie (Brown and Smith 2000). We extend this regime description to include temporally- explicit mixed- severity fires that create a mosaic of living and dead vegetation in lightly, moderately, and severely burned areas within the fire perimeter. The effects of mixed- severity wildfires have become a critical question in the Black Hills, SD, USA, following the fire season of 2000, in which 6 fires burned ~39000 ha of ponderosa pine-dominated *(Pinus ponderosa var scopulorum)* forests and grasslands. The largest of these fires, the Jasper fire, burned ~34,000 ha, exhibiting variable burn severity and creating a mosaic of vegetative mortality across the landscape. The Jasper fire, like other recent, large wildfires (e.g. the Yellowstone fires, WY, 1988, the Hayman fire, CO 2002, the Rodeo-Chedeski fire, AZ 2002, and the Biscuit fire, OR and CA, 2002) did not consume the entire forest; however, the landscape imprint of the Jasper Fire may be quite different from other large fires outside the Black Hills due to the prevalence of mixed-mode burning under extreme weather conditions. The fine-grained pattern of living and dead vegetation in patches ranging from square meters to thousands of hectares has major implications for recovery processes in areas of different burn severity. Ecological interpretation of fire effects may be different in areas impacted by different burn severity and the spatial arrangement of burned patches has important management relevancy. The scale and heterogeneity of the Jasper fire provides an opportunity to compare fire effects on soil and vegetation in areas of different burn severity and to explore management alternatives in the Black Hills.

We developed two research questions to guide our study of immediate and delayed fire effects on vegetation, litter, and soil. First of all, were fire effects on resources similar or different in areas of different burn severity? Fire effects actually occur along a spectrum of low to high severity and depend largely on fire behavior and the fuels available for burning (DeBano et al. 1998). For this reason, we expected that the direct effects of low, moderate, and high- severity fire would differ, although high variability may be inherent in any study including burn severity as a predictor variable. Some resources may be extremely sensitive to fire of any severity, while some fire effects may be clearly discernable in areas of different burn severity. While this may seem simple and straightforward at first, the variability of initial fire effects may help to explain response complexity. Secondly, we asked how do resources respond in areas of different burn severity over time? Burn severity is not a single quantitative measure of resource impact, but refers to relative magnitudes of fire impacts (DeBano et al. 1998); therefore, we expected that areas affected by different burn severity would function very differently over time. Some aspects of resource recovery may occur within a few years post-fire, but others may take a very long time to recover pre-burn conditions. Currently, there are several previously burned areas on the Black Hills landscape that have been devoid of vegetation for many decades, and we expect structural and compositional heterogeneity may reflect the occurrence of the Jasper fire for many years to come.

In order to quantify the immediate and the delayed effects of fire and to characterize burn severity, we addressed the following questions:

1) Are fire effects on trees and rates of mortality different in areas of different burn severity? The magnitude of fire effects on tree roots, boles, and crowns or a combination of injuries usually determines post-fire tree mortality (Herman 1950; Dieterich 1979; Peterson 1985; Wyant et al. 1986; Harrington 1987; Ryan and Frandsen 1991). Stand density, tree diameter, and surface fuel consumption, especially around the base of the tree, may also predict mortality (DeBano et al. 1998; Brown and Smith 2000). We expected that immediate tree mortality would be greatest in areas experiencing extensive crown consumption and scorch, but delayed mortality would be greatest in areas of severe surface burning. We also expected that smaller diameter trees might be more vulnerable to fire-kill due to thinner bark or crown injury (Gutsell and Johnson 1996; Brown and Smith 2000). Alterations to light and nutrient regimes following tree death may have major implications for understory plant and seedling recovery in burned stands.

Crown injury reduces tree vigor; however, massive seed release or a large pulse of germination may follow fire (Whelan 1995). The potential for seedling recruitment due to canopy disturbance and improved seedbed conditions is related to burn severity (Lyon and Stickney 1974; Sackett 1984; DeBano et al. 1998), although seed dispersal may limit forest reestablishment. Seed production, and therefore, seedling densities are temporally and spatially variable, and likely influenced by post-fire climate (Whelan 1995). We expected seedling regeneration to be greatest in moderate severity patches due to substantial disturbance to the canopy and forest floor in the presence of surviving, seed-producing trees.

2) How much litter, duff, and downed woody material was consumed in areas of different burn severity, and what is the rate of fine and large woody material accumulation as scorched needles are shed and snags break and fall? The accumulation of fine and large woody fuels may lead to increased burn severity, and high burn severity may contribute to the buildup of large woody material (Jurgensen et al. 1997; DeBano et al. 1998). We expected greater reductions of litter, duff, and downed woody material in areas of higher burn severity followed by variable rates of re-accumulation. Litter re-accumulation might be highest in areas of greatest crown scorch, but lowest where needles were consumed. Small and large downed woody material re- accumulation would be greatest in areas of high burn severity as dead trees fall.

3) How were total soil carbon and nitrogen affected by different burn severity, and how quickly does soil nitrogen availability return to prefire conditions? More severe fire results in a greater loss of organic matter on the surface or in the soil (DeBano et al. 1998). Combustion of organic matter, the primary source of most available nitrogen, causes rapid volatilization of nitrogen. Total and available soil nitrogen concentrations have been reported to increase, decrease or stay the same following fire (Wells et al. 1979, DeBano et al. 1998). We expected greater reductions in total soil carbon and nitrogen and higher concentrations of available soil nitrogen in areas of high severity

immediately following fire. We expected soil nitrogen availability to decline in response to plant re-establishment.

4) How was plant cover and species richness affected by different burn severity? How long until plant cover returns to pre-fire levels, and how did fire influence species composition? Burn severity influences injury and mortality of plants and the rate of reestablishment of resprouting species (Lyon and Stickney 1976; Ryan and Noste 1985; Debano et al. 1998). Canopy and seedbed conditions are altered by fire and whether these conditions are favorable depends upon the characteristics of the plant species on the site, their susceptibility to fire, and the means by which they recover after fire (Mutch 1970; Lyon and Stickney 1976; Anderson and Romme 1991; Turner et al. 1998). The length of time that a seed environment retains these conditions after fire determines the number of post-fire years that establishment of certain species from seed can take place (Wagle and Kitchen 1972; Shearer and Stickney 1991; Turner et al. 1998). Plant regeneration may occur from on-site seeds, from off-site seed sources, or from deeply buried and protected root structures. We expected greater reductions in plant cover in areas of more severe fire, and regeneration from root stock to be more critical in severely burned areas. We expected more rapid recovery of plant cover and less dramatic shifts in species composition in low and moderate burn severity patches due to on-site seed sources. A better understanding of differential plant mortality and rates of reestablishment in areas of different burn severity will improve our understanding of the ecological consequences of large, mixed- severity fires.

METHODS

2.1 Jasper Fire

The Jasper fire was the largest recorded fire in the history of the Black Hills. The Jasper fire was human-caused and spread rapidly, overpowering initial attack suppression forces. Weather conditions were very hot and dry, fuel moisture conditions were at record low levels, and atmospheric conditions were very unstable, resulting in extreme fire behavior. On the first day, the fire doubled in size every hour, consuming ~1500 ha within four hours. Almost immediately, the fire spread into the crowns of trees, and spot fires formed ahead of the main fire. On the third day, the fire exploded into a plume-dominated fire, growing at an average rate of more than 40 ha min^{-1} and burning over 18000 ha in a few short hours (JRAT 2000). Twelve days and $8.2 million later, the Jasper fire was officially contained after burning ~ 7% of the landbase of the Black Hills National Forest.

The Black Hills is an isolated mountain range on the Northern Great Plains physiographic province in western South Dakota and northeastern Wyoming (Boldt and Van Deusen 1974; Shepperd and Battaglia 2002). As the easternmost extension of the Rocky Mountains, the Black Hills was formed by regional uplift between ~35 to 65 several million years ago. This uplift produced an elliptical dome with an older crystalline core surrounded by younger, steeply dipping sedimentary deposits (Froiland 1978). The Limestone Plateau surrounds the core and the area burned by the Jasper fire is located on the southwestern extent of this fertile plateau.

Interior ponderosa pine stands in various successional stages form the dominant vegetation matrix, but scattered aspen (*Populus tremloides*) clones and meadowland inclusions are found in the study area. Ponderosa pine is relatively shade-intolerant, has a strong tendency to form even-aged stands, and is a reliable seed producer with good seed years occurring every 2-5 years. Natural regeneration is abundant and relatively constant due to favorable moisture conditions throughout the spring and summer. Ponderosa pine stands are typically managed under the two-cut shelterwood system with timing of the removal cut based on regeneration establishment and development. (Shepperd and Battaglia 2002).

Wildfire suppression, grazing, logging, and attempts to control mountain-pine beetle outbreaks in the time since settlement (~ 1880's) have resulted in changes in forest composition, structure, and ecosystem attributes in the Black Hills. The two most important changes relate to simplification of vegetative diversity and forest structure. Understory plant biomass and species richness have declined as a result of increases in ponderosa pine canopy cover and cattle grazing. Snag densities and large, downed woody biomass have decreased as timber removal has occurred over most of the forest. Smaller woody biomass and fine fuels have increased over much of the forest with effective fire suppression. Persistent harvesting over the past century, coupled with insect, disease, wind and ice-related mortality, and fire suppression, has resulted in the conversion of the old-growth pine forest to a relatively homogenous, heavily stocked, second-growth forest with a high degree of fuel build-up and continuity (USDA 1997).

2.2 Experimental Design

We used existing forest Geographic Information System (GIS) and Resource Inventory System (RIS) databases, project plans, and input from the Black Hills fire specialists to identify study areas within the Jasper fire. We identified three ~800 ha study areas that contained a mosaic of fire behaviors within the north, central, and southern portions of the fire perimeter where management activities were limited to roadside hazard tree removal and spot spraying of noxious weeds.

Following fire, the appearance of vegetation, litter, duff, and upper soil horizons can be used to estimate the amount of heat radiated downward into the underlying duff and mineral soil (DeBano et al. 1998; Ryan and Noste 1985). The magnitude of the observed change depends largely on the severity of the fire. We used color infrared aerial photography, a GIS-based map of canopy scorch, and relative magnitudes of burn severity, expressed in terms of post-wildfire appearance of vegetation, litter, and soil, to place burn severity into broadly defined, discrete classes of low, moderate, and high (Table 1). Study sites were replicated three times within each burn severity class within each of the three study areas for a total of 36 study sites (Table 2). Three unburned study sites were established near each of the study areas to provide reference for pre-fire conditions.

2.3 Field Sampling

In early 2001, we established 0.28 ha study sites in 27 burned and 9 unburned pine stands. We visited each study site in May, 2001, and thereafter in July- August, 2001 to 2003 to record measurements and collect information.

At each study site, we established a study site center. We recorded study site center coordinates with a Garmin™ Global Positioning System (GPS) unit. Twenty meters from each study site center at 0°, 135°, and 225° bearings, we established three 0.03 ha plots. On plots, we collected information about trees, light transmission, seed production, and soil nutrients. We established 30 m line transects at 90° and 270°

bearings with the site center as midpoint. On each transect, we measured vegetation, forest floor litter, and dead and down woody material with a variety of fixed areas plots. On each study site, we collected information about regeneration (Fig. 1).

2.3a Plot sampling

In each plot, we tagged every tree > 1.4 m tall. For each tree, we assessed species and live/dead status. We measured diameter at breast height (DBH). We used an Impulse® laser hypsometer to record pre-fire live crown length and tree height. We revisited tagged trees in 2002 and 2003 to evaluate status.

In each plot, we estimated beneath-canopy light intensity by measuring light flux density with a sunfleck ceptometer (Decagon Devices, Inc., Pullman, WA). We collected readings in cardinal directions at 10 points per plot and calculated an average for each site. We collected readings in a nearby forest opening with an unobstructed view of full sunlight assumed to represent above-canopy readings. "Open" readings were obtained every 15 minutes and averaged over the sampling period. Light sampling was conducted on sunny days between 1000 and 1400 hr MST during June- July, 2001-2003. These readings provide an estimate of the amount of canopy disruption in areas of different burn severity.

We installed 2 covered wire seed traps (0.2296 m^2) on each plot. We installed one uncovered trap (0.2296 m^2) per plot at one site in each burn severity class per study area to monitor seed predation. In 2002 and 2003, seed traps were emptied and replaced for collection the following year. Contents collected from the traps were sorted and pine seeds were counted in the laboratory at Colorado State University.

We collected soil samples from a 0.025 m^2 surface area to a depth of 10 cm (~2560 cm^3 ± rock volume) at 2 points on each plot. Soil samples were oven-dried at 60°C. Soil samples were passed through a 2-mm sieve and the fractions greater and < 2 mm were weighed. We measured total soil organic carbon and nitrogen using a Leico™ CHN analyser. We used ion exchange resin bags to estimate soil nitrogen availability (Binkley et al. 1995).

2.3b Transect Sampling

We estimated total kg ha^{-1} of fine woody fuels (<7.6 m) and downed woody biomass (>7.6 m) using the planar intersect method (Brown et al. 1982). Fine woody material (<7.6 m) was measured on 10 m and downed woody biomass (>7.6 m) was measured on 40 m of transects. We measured litter and duff depths at 30 points located at 2 m intervals along transects.

We inventoried vegetation in six 0.25m^2 plots located at 10 m intervals offset from transects on each study site. Within each plot, we recorded plant species or cover type (exposed mineral soil, litter, rock, or woody material) and visually estimated percent cover. We excavated ten specimens per study site of each species found in understory plots to determine whether individuals survived the fire or germinated post-fire.

We surveyed regeneration in fifty 1.0 m^2 (0.0001 ha) plots on each study site. We counted the number of seedlings < 1.4 m in height and determined seedling age.

2.3c Sampling of Direct Fire Effects

We measured crown scorch, crown consumption, bole scorch, basal scorch and basal char on individual trees in plots. We used an Impulse® laser hypsometer to record minimum and maximum heights of crown scorch and crown consumption. We visually estimated the portion of the crown scorched or consumed within this area to the nearest 5%. We determined the percent of crown scorched or consumed relative to the entire live crown length from these measurements. We measured the maximum height of bole scorch and determined the percent of the bole affected by scorch relative to total tree height. We measured the percent of the bole circumference scorched at 1m height. We measured basal scorch and basal char as the percent of the bole circumference either scorched or charred at heights less than 30 cm. Scorched bark was intact and gray-black in color, with distinguishable furrows, and a flaky texture. Charred bark was often partially eroded by fire and metallic black in color, with undistinguishable furrows, and texture similar to that of charcoal.

We visually assessed the percent low, moderate, and/or high ground char (Ryan and Noste 1985) for a 0.025 m^2 surface area at 30 points located at 2 m intervals along transects at each study site. We indexed burn severity as the product of the proportion of the ground area charred and the degree of char scaled from low (1) to high (3). We visually estimated the proportion of the ground that was burned within each 1.0 m^2 (0.0001 ha) regeneration plot.

2.4 Statistical Analysis

We performed all summary and statistical analyses in SAS® V 8.2 (SAS Institute 2001). Trees < 5 cm DBH were not included in the analysis. We compared values in an ANOVA model (PROC GLM, SAS Institute, 2001). Variables were tested for significance at the 95% confidence level (alpha = 0.05). We included burn severity and study area location as independent variables in all model analysis. If study area location was a statistically significant predictor then reported p-values include its effect.

RESULTS

Our study sites were well-stocked ponderosa pine stands prior to the Jasper fire. Average stand diameter (ASD) was 21.8 cm and mean tree height was 12.7 m. Mean densities were 713.1 trees ha^{-1}, mean basal area (BA) was 24.7 m^2 ha^{-1}, and relative density was ~ 46 % of maximum stand density index. Stand structures were not significantly different in terms of tree size, density, or basal area in unburned and burned sampling areas ($P < 0.05$) (Table 4).

3.1 Direct fire effects on trees and tree mortality

The direct and cumulative effects of fire on trees were much greater on high severity than on low or moderate severity study sites. The entire bole was scorched, and canopy foliage and small branches were completely consumed in areas of high- severity fire. Bole and crown scorch was more extensive on moderate than on low severity study sites. We found that ~75 % of the crown was scorched or consumed on moderate severity as compared to ~ 20% on low severity study sites. On average 80% of the base of each tree bole was scorched on low and moderate study sites, and we observed 2.2 times more char on the base of each tree on moderate severity study sites. Fire effects on trees including crown scorch and consumption, bole scorch at 1 m and on the entire tree, and basal scorch and char were statistically different in areas of different burn severity (Table 5).

Tree mortality was related to burn severity and continues to increase in areas with surviving trees. All trees were killed on high severity study sites due to direct fire injury.

We initially observed < 1 % tree mortality on low severity study sites, but found ~ 23 % of trees were killed by fire on moderate severity study sites. Surviving trees on moderate severity study sites were more likely to die over time. Tree mortality increased substantially for 3 years following fire when compared to immediate post-fire observations. Cumulative 3-year mortality increased to 16% on low severity and 59% on moderate severity study sites. Tree mortality was significantly different on study sites of different fire severity one, two, and three years post-fire ($P < 0.05$).

Fire selectively killed smaller diameter trees in areas of low and moderate burn severity, and no trees, regardless of diameter, survived in areas of high burn severity. Average DBH of dead trees in low severity was 8.3 cm the first year after fire, increasing to 16.7 cm for trees dying in the third year. In moderate severity, where initial mortality rates were greater, trees dying in the first year averaged 16.9 cm DBH and increased to 21.4 cm in the third year post-fire. Trees with the smallest diameters in the population of surviving trees died over time (Table 5). Moderate severity fire killed larger trees, and larger trees took longer to die. Tree diameter of trees surviving one year post-fire was not significantly different on low and moderate severity study sites ($P < 0.05$). Tree diameter of fire-killed trees was significantly different on low, moderate, and high severity study sites ($P < 0.0001$) one year post-fire. Two and three years post-fire, tree diameter of surviving trees was significantly different on low and moderate severity study sites ($P < 0.05$). Two and three years post-fire, tree diameter of dead trees was significantly different on low and moderate severity study sites ($P < 0.01$).

Crown consumption causes an immediate reduction in canopy cover; however, scorched needles may not fall immediately. One year post-fire, 44, 53, and 78 % of full sunlight reached the forest floor on low, moderate, and high burn severity study sites, while 25 % of full sunlight reached the forest floor on unburned study sites. Approximately 3 times more light reached the forest floor on high severity study sites as compared to unburned study sites. On low and moderate study sites, 1.8 and 2.1 times more light reached the forest floor than on unburned study sites. Light transmission was significantly different in burned and unburned areas ($P < 0.0001$) and in areas of different burn severity ($P < 0.05$) one-year post-fire. Two years post-fire, 49, 60, 73 % of full sunlight reached the forest floor on low, moderate, and high burn severity study sites, while 49 % of full sunlight reached the forest floor on unburned study sites. Three years post-fire, 52, 73, 82 % of full sunlight reached the forest floor on low, moderate, and high burn severity study sites, while 43.4 % of full sunlight reached the forest floor on unburned study sites. Two and three years post-fire, canopy interception of sunlight was significantly different between unburned and burned sites ($P <0.001$). In both years, canopy light interception was significantly different in areas of different burn severity ($P < 0.0001$).

We explored the relationship between light transmission and live basal area. Light penetration increased in areas of higher tree mortality, although in areas of complete tree mortality ~ 23 % of light was intercepted by standing dead tree boles. We found a strong negative relationship between light transmission and live basal area in all years following fire. Live basal area explained ~ 49% of the variation that we saw in light transmission over time.

3.2 Fire effects on litter and rates of re-accumulation

Fire effects on the forest floor were most substantial in areas of high burn severity where litter and duff were almost completely consumed. Burn index was 119 on low, 186 on moderate, and 246 on high severity study sites on a scale of 100 to 300 (Fig. 9). Burn index was statistically different in areas of different severity ($P < 0.0001$). We found average litter depths of 1.2, 0.5, and 0.2 cm on low, moderate, and high severity compared with 4.8 cm on unburned study sites. Fire reduced litter depths by ~ 76, 91, and 97% on low, moderate, and high severity study sites one year post-fire. On average, there were 2.3 and 6.6 times more duff on unburned study sites than on low and moderate study sites. No duff remained on high severity study sites. Litter depth was significantly different when comparing unburned and burned study sites ($P < 0.0001$) and on study sites of different burn severity ($P < 0.0001$).

Three years post-fire, litter depths were similar on low and moderate severity sites, although initial reductions were greater on moderate severity study sites. We observed the greatest change in litter depths on moderate severity study sites as scorched needles were shed. Litter depth increased to 2.2 cm on low and moderate severity sites and 0.6 cm on high severity sites compared to 5.6 cm on unburned study sites. Three years post-fire, litter depth was ~ 60% lower in areas of low and moderate severity and 90% lower in areas of high severity when compared with similar unburned stands. Litter depth was statistically different when comparing unburned and burned study sites ($P < 0.0001$) and in areas of different burn severity ($P < 0.0001$) two and three years post-fire.

3.3 Fire effects on fuel loadings and rates of re-accumulation

Fire consumption of dead and down woody material was not strongly related to burn severity. We found 7315, 10233, 6273 kg ha^{-1} on low, moderate, and high severity sites compared with 24,831 kg ha^{-1} on unburned study sites. Fire reduced dead and down woody material on the forest floor by ~ 71, 59, and 75% on low, moderate, and high severity study sites. Mean fuel loadings were ~ 3 times higher on unburned than on burned study sites. On unburned sites, fine fuels (material < 7.6 cm in diameter) and large fuels (> 7.6 cm in diameter) comprised 23% and 77% of total fuel weight. For all burned study sites, fine fuels and large fuels were 21-34% and 66-79% of total fuel loadings. Total fuel loads were significantly different on unburned and burned study sites ($P < 0.0001$), but were not significantly different on study sites of different burn severity ($P < 0.05$). Fine fuels loads were significantly different in areas of different burn severity ($P < 0.001$). Large fuels loads were not significantly different in areas of different burn severity ($P < 0.05$).

In the second and third years post-fire, we found much lower rates of dead and down woody material accumulation on low and moderate severity sites compared to high severity study sites with complete tree mortality. The cumulative total of dead and downed woody material was similar on low and moderate severity study sites, although accumulations on moderate severity sites were unchanged during the first three years following fire. We found 10392, 10810, and 18017 kg ha^{-1} on low, moderate, and high severity sites compared with 24,955 kg ha^{-1} on unburned study sites (Fig. 5). Three years post-fire, dead and down woody material on the forest floor was ~ 58, 57, and 28% lower on low, moderate, and high severity sites than on unburned study sites. The composition (fine vs. large) fuels was unchanged two and three years post-fire. Two years post-fire, total fuel loads were significantly different on unburned and burned study sites ($P < 0.01$), but were not significantly different on study sites of different burn severity ($P < 0.05$). Three years post-fire, total fuel loads were significantly different on unburned and burned study sites ($P < 0.001$) and on study sites of different burn severity ($P < 0.05$). Fine fuels loads were significantly different in areas of different burn severity ($P < 0.05$) two and three years post-fire. Large fuels loads were not significantly different in areas of different burn severity ($P < 0.05$) two and three years post-fire.

3.4 Fire effects on soils

Organic carbon was 32 and 28 % lower in burned than in unburned soils one and two years post-fire. Organic nitrogen was 13 and 16 % lower in burned soils than in unburned soils one and two years post-fire. In both years total soil carbon was significantly different on unburned and. burned study sites ($P < 0.05$). Total soil nitrogen was not significantly different on unburned and. burned study sites ($P < 0.05$) in either year.

The amount of nitrogen available for plant uptake increased immediately following fire, but rapidly became less available. The total nitrogen available to plants in the form of nitrate was 85 and 21 times greater on burned than on unburned sites one and two years post-fire. Total nitrogen available to plants in the form of ammonium was 3 and 2 times greater on burned than on unburned sites one and two years post-fire. Ninety-four percent of nitrogen available for plant uptake was in the form of nitrate. Neither total nitrate nor total ammonium available to plants were significantly different on burned and unburned study sites or on study sites of different burn severity one year post-fire ($P < 0.05$). Total nitrate was significantly different on burned and unburned study sites and on study sites of different burn severity two years post-fire ($P < 0.05$). Total ammonium was not significantly different on burned and unburned study sites ($P < 0.05$), but was significantly different on study sites of different burn severity two years post-fire ($P < 0.0001$).

3.5 Fire effects on plant cover and composition

We observed substantial reductions in vegetation cover and species richness immediately following fire (Table 6). Plant cover was 13, 6, and 2 % on low, moderate, and high severity sites compared to 38 % on unburned study sites. Plant cover on low and moderate severity study sites was ~35 and 84 % lower than on unburned study sites. Plant cover was ~ 95% lower on high severity sites than on unburned study sites. Species richness was similar on unburned and low severity sites, with about 40 species present. However, richness declined to 22 species on moderate and 26 species on high severity study sites. On unburned study sites, shrubs contributed 58 % of total plant cover. Forbs and grasses each contributed an additional 20 % of total cover. On low severity study sites, forbs contributed 51 % of total plant cover. Grasses and shrubs each contributed 37 and 11 % of total cover. On moderate severity study sites, forbs contributed 69 % of total plant cover. Grasses and shrubs contributed 26 % and 5% of total cover. On high severity study sites, forbs contributed 58 % of total plant cover. Grasses and shrubs provided 17 and 25% of total plant cover. Shrubs were reduced and forbs were increased as a percentage of total cover by fire in all severity classes (Table 6).

A majority of newly regenerating plants in burned areas originated from existing root stock. We surveyed ~ 1300 individuals per burn severity class and found 73, 63, and 56 % regenerated from root stock on low, moderate, and high severity sites. Most shrub species re-sprouted following fire, and 82-92 % of specimens regenerated from root stock. Grass species were also likely to have survived the fire and 75-85 % regenerated from root stock. Forbs were most likely to have regenerated from seed, and 46-65 % of specimens did not regenerate from root stock. The proportions of grasses and forbs that regenerated from root stock were significantly different in areas of different burn severity ($P < 0.05$). The proportion of shrubs that regenerated from root stock was not significantly different in areas of different burn severity ($P < 0.05$) (Table 7).

Plant cover increased substantially during the first growing season although total cover remained lower than pre-burn cover estimates. Plant cover was 25, 18, and 11 % on low, moderate, and high severity study sites. Plant cover increased by ~57% on low and moderate severity study sites during the first season following fire, but was ~43 % lower than on unburned study sites. Plant cover increased by 80% on high severity study sites during the first growing season post-fire, although cover remained ~ 71% lower than on unburned study sites. Vegetation cover approached pre-burn total cover levels two years after the fire. Plant cover was 48, 41, and 37 % on low, moderate, and high severity study sites compared to 51% on unburned sites two years post-fire. Plant cover was 7 % lower on low severity sites than on unburned study sites. Plant cover was 20 % lower on moderate and 27% lower on high severity sites than on unburned study sites. Vegetation cover was higher on moderate and high severity study sites than on unburned study sites three years post-fire. Plant cover was 50, 66, and 58 % on low, moderate, and high severity study sites compared to 52% on unburned study sites three years post-fire. Plant cover was ~ 9 % higher on moderate and high severity sites than on unburned study sites. Plant cover on low severity study sites was ~ 6 % lower than on unburned study sites. Total cover relative to unburned cover estimates indicates that recovery in burned understory plant communities occurs within three years following fire.

Species richness returned to pre-burn levels in burned areas one year post-fire. Two years post-fire, species richness on low and high severity study sites was equal or greater than species richness on unburned study sites. Three years post-fire, species richness on low and moderate study sites was equal or greater than species richness on unburned sites. Species richness was lower on high severity study sites than on unburned sites. Species richness estimates indicate inter-annual variability and, while certain species present before the fire are absent in post-fire understory communities, overall richness recovered one year post-fire.

Species dominance by functional plant type cover was different in the post-fire environment. Plant cover was dominated by forb species on all burned sites during the first three years post-fire. Shrub species cover continued to be much lower on burned than unburned sites, while forb cover was 33 to 52% higher on burned than on unburned study sites. Shrub species provided almost half of plant cover on unburned study sites; however, forbs provided over half of total cover on burned sites. On unburned study sites, shrubs, forbs, and grasses contributed 45, 29, and 23 % of total plant cover three years post-fire. On burned study sites, forbs contributed 43 to 63 % of total cover, grasses contributed 11to31 %, and shrubs contributed 13 to 28 % of total plant cover three years post-fire. Changes in species dominance by functional plant type were similar on all burned sites and consistent during the first three years post-fire.

3.6 Seedling Recovery

Seedling regeneration and seed production was limited and variable following fire. Eighty-six, 95, and 97 % of the ground was burned on regeneration plots on low, moderate, and high severity study sites, although the degree of ground char was relative to severity. We found 1156, 1067, and 44 seedlings ha^{-1} on low, moderate, and high severity study sites compared to 13,089 seedlings ha^{-1} on unburned study sites. The number of potentially viable seeds produced one year post-fire in unburned areas was ~16 % greater than in burned areas. Seed production was 22, 65, and 48 % lower on low, moderate, and high severity sites than on unburned study sites. Seed predation rates were ~ 32 % in unburned areas. Seed predation rates were ~ 8 % on low and moderate severity sites and 75 % on high severity sites. Seedling regeneration was significantly different on unburned and burned sites ($P < 0.001$), but not significantly different on study sites of different burn severity ($P < 0.05$) one year post-fire.

Cumulative regeneration densities increased on all burned sites two years post-fire. Regeneration densities were 1400, 2456, and 122 seedlings ha^{-1} on low, moderate, and high severity study sites two years post-fire compared with 9380 seedlings ha^{-1} on unburned study sites. The number of potentially viable seeds produced two years post-fire was ~10 % greater in burned areas than in unburned areas. Seed production was 15 % higher, 41 % lower, and 17 % higher on low, moderate, and high severity study sites than on unburned sites. Seed predation rates were 65 % on unburned sites compared with 23 % on low severity study sites. All seeds were predated on moderate and high severity study sites (Fig. 7). Seedling regeneration was significantly different on unburned and burned sites and on study sites of different burn severity ($P < 0.01$) three years post-fire.

We found low regeneration densities on low and moderate study sites three years post-fire compared to one and two years post-fire, and essentially no regeneration on high severity sites. We found 568, 533, and 11 seedlings ha^{-1} on low, moderate, and high severity study sites compared with 8413 seedlings ha^{-1} on unburned study sites. Seedling regeneration was not significantly different on unburned and burned sites ($P < 0.05$), but was significantly different on study sites of different burn severity ($P < 0.001$) three years post-fire. Low seed production coupled with high predation in the first two years post-fire has resulted in much lower seedling densities on burned sites compared to unburned sites.

DISCUSSION

Following a single, mixed- severity wildfire in the Black Hills, we found considerable variability in fire effects over a large area. While heterogeneous effects have been documented following other large wildfires, (Lyon and Stickney 1974; Whelan 1995; DeBano et al 1998; Turner et al. 1994; Turner and Romme 1994; Turner et al. 1997; Turner et al. 1998; Graham 2003; USDA 2002, 2003), the landscape imprint of the Jasper fire was distinctly different. Spatial analysis of a map of burn severity derived from Landsat 7 imagery taken in 2001 indicated a highly patchy mosaic where 25, 48, and 27 % of the landscape was burned by low, moderate, and high- severity fire. Although ~ 60 % of the total acreage burned in less than 12 hours, burn severity was variable and patches of low, moderate, and high burn severity were relatively evenly distributed on the landscape.

Burn severity and patch size exert an important influence on plant succession following fire. Large patches of high- severity fire are likely to have few resprouting species and more of the canopy and seedbank destroyed (Turner et al. 1994; Graham 2003). Patch sizes in the Jasper fire were small relative to total daily area burned, and largest patch sizes were 1550, 3500, and 900 ha in areas of low, moderate, and high severity. Based on the cumulative distribution of patch sizes, ~ 55 % of the area in low and moderate severity patches was greater than 250 ha in size, yet 60 % of the area found within high severity patches was less than 50 ha in size (Lentile Dissertation Chpt. 1). In contrast, high- severity fire impacted ~ 24,000 ha, roughly half of the landscape burned by the Hayman fire. Small "escapes" or narrow "tree crown streets" were embedded within large patches of crown fire in these montane ponderosa pine (*Pinus ponderosa* var. *laws*) and Douglas- fir (*Pseudotsuga menzensii*) forests. Patch sizes were also large (~ 3500 ha) following the Yellowstone fires, and crown fire burned 31 % or ~ 70,000 ha in these subalpine lodgepole pine (*Pinus contorta* var. *latifolia*) forests (Turner et al. 1997). In each of the Rodeo-Chedeski and Biscuit fires over 30,000 ha were burned by high-severity fire creating extensive patches where all trees were killed (USDA 2002, 2003). The proportion and patch sizes of high- severity fire were much smaller in Jasper; and rather than patches of surviving vegetation within a matrix of crown fire, a matrix of surviving vegetation was interspersed with patches of crown fire on the Jasper landscape.

The heterogeneity of fire effects and distance from living vegetation differentially impact species with certain life strategies and influence successional trajectories (Pickett and White 1985; Turner et al.1997). Following the Yellowstone fires, Turner et al. (1994) found that smaller patches were often more variable in fire effects and less severely burned, and larger patches were more likely to be less variable in effects and severely burned. In contrast, we found large patches were often more heterogeneous in fire effects and less severely or moderately burned. Low and moderate severity patches averaged ~ 10 and 24 ha in size and were within 10 m of a green edge. High severity patches were small, averaging ~8 ha in mean size, and 55 % of the area that burned under high severity was within 30 m of a potential tree seed source in adjacent low or moderate severity patches.. In Yellowstone, 25% of the area burned by crown fire was greater than 200 m from unburned or lightly burned areas (Turner et al.1994). In Jasper, 99% of the area that burned under high severity was within 200 m of a green edge. The juxtaposition of low, moderate, and high severity patches in the Jasper fire mitigated the effects of high- severity fire by providing nearby herbaceous and tree seed sources and likely increased rates of plant recovery.

The spatial pattern of burn severity caused by a large wildfire in the Black Hills was different from those created by wildfires in other regimes. But, how different were fire effects in areas of different burn severity within this mixed- severity fire? We found that some resources were not particularly sensitive to magnitudes of burn severity and were affected similarly in all burned areas; however, most fire effects were strongly related to burn severity. Vegetation mortality and light, nutrient, and microsite availability increased relative to burn severity. Reductions in soil carbon and nitrogen and large downed woody material were independent of burn severity. Rates of recovery were variable in areas of different fire severity. Some aspects of recovery such as understory plant cover and tree mortality changed significantly during three years post-fire, and, other aspects such as seedling recovery were little changed.

Post-fire responses depend upon the characteristics of the plant species on the site, their susceptibility to fire, and the means by which they recover after fire (DeBano et al.

1998). Many herbaceous and shrub species can regenerate from seed and from rootstock (Lyon and Stickney 1976, Stickney 1986, Anderson and Romme 1991). Our data concur with studies that suggest the strong influence of pre-fire stand structure and species composition on post-fire vegetation development (Lyon 1976, Lyon and Stickney 1976, Anderson and Romme 1991; Turner et al. 1997). Lyon and Stickney (1976) found that 86 % of individuals dominant in lodgepole pine stands in the first few years after fire were present before the fire, and 75 % regenerated from rootstock. Anderson and Romme (1991) found that 67 % of post-fire species survived the fire and that all regenerated from rootstock. Our data indicate that 60 % of species initially found on burned sites were present before the fire and ~ 70 % of all species regenerated from rootstock. Plant survival and post-fire resprouting has been related to differences in depth distribution of rhizomes in soil (Granstrom and Schimmel 1993; Turner et al. 1997). Surviving vegetation may also produce seeds and facilitate germination or, alternatively, exert a competitive influence.

Plant cover decreased with increasing burn severity. We found significant differences in total plant cover in areas of low, moderate, and higher severity immediately after fire. Plant cover increased through time, although species composition was drastically changed. Plant cover increased 4, 11, and 18 times in low, moderate, and high severity areas between 2001 and 2003. Three years post-fire, cover was highest in severely burned areas, although fewer species contributed this cover. Species richness was lower in larger and more severely burned patches in Yellowstone; although, more severe abiotic conditions, and not reduced seed dispersal, may have been responsible for this decline (Turner et al.1997). Plant recovery to pre-fire conditions following the

Jasper fire was likely more rapid than has been observed in other large fires due to the absence of large patches of high- severity fire and the high number of species regenerating from rootstock.

In general, areas most susceptible to nonnative plant invasion are also more favorable for native species plant recovery (Stohlgren et al.1999; Stohlgren et al. 2002; Graham 2003). Large patches of crown fire provided the best colonization sites for opportunistic species following the Yellowstone fires (Turner et al.1997). We found three times more nonnative species in low and moderately burned areas than in unburned or severely burned areas two years post-fire. Three years post-fire, we found similar numbers of non-native species in all burned areas. Canada thistle (*Cirsium arvense*), houndstongue (*Cynoglossum officinale*), and common mullein (*Verbascum thapsus*) were consistently found in all burned areas. The length of time after fire that a seed environment retains high resource availability and low competitive conditions determines the number of post-fire years that establishment of certain species from seed can take place (Shearer and Stickney 1991).

In the first three years post-fire, we found understory plant communities dominated by weedy annual forb species. Five years after the Yellowstone fires, biotic cover and species richness of forest herbs was lower in large patches of high- severity fire than in smaller, less severely burned patches (Turner et al. 1997). We found the survival of grasses and forbs increased along the burn severity gradient from high severity to low severity, and that initial recovery was more rapid in less severely burned areas. We found 75 % of grasses, predominantly strongly rhizomatous Carex spp., were present before the fire. In burned areas, weedy annual forbs such as lamb's quarters

(*Chenopodium album*), horseweed (*Conyza canadensis*), and prickly lettuce (*Lactuca serriola*) and taprooted or rhizomatous perennial species such as arrowleaf balsamroot *(Balsamorhiza sagittata)*, American licorice (*Glycyrrhiza lepidota*), and dogbane (*Apocynum androsaefolium*) contributed > 75 % of forb cover. These species replaced prominent groundcover species like small-leaf pussytoes (*Antennaria parvifolia)* in all burned areas. Our data show that within two years post-fire herbaceous cover approaches or exceeds pre-burn estimates in all burned areas, thus limiting opportunities for seeds to establish.

Shrub cover was uniformly low in all burned areas immediately after fire. We observed almost complete removal of aboveground plant parts of shrubs, independent of burn severity, but found 83 % of shrub species regenerating in post-fire communities were present in pre-fire communities. Almost all shrub recovery observed following the Jasper fire was vegetative. Common juniper (*Juniperus communis*) provided 93 % of pre-fire shrub cover and was noticeably absent in burned areas due to its inability to sprout from rootstock. Roots of mature juniper are in the litter and upper soil layers where they are especially sensitive to fire damage. Shrub cover was substantially reduced following fire in Yellowstone and showed no significant change in five post-fire years. We found shrub cover was ~ 40 % of pre-burn cover levels in less severely burned areas; however, shrub cover was almost two times greater in severely burned areas than in less severely burned areas three years post-fire. We found two shrub species, mountain ninebark (*Physocarpus monogynus*) and shrubby cinquefoil (*Potentilla fruticosa),* in severely burned areas that were not present in less severely burned or unburned areas.

Fire reduced total organic carbon and nitrogen uniformly, however, the amount of nitrogen available for plant uptake increased with increasing burn severity. We found soil nitrogen availability was 21 to 41 times greater in low and high severity patches than in unburned areas one year post-fire, and variability of nitrate was extremely high among samples one year post-fire. Two years post-fire, soil nitrogen availability was 6 to 20 times greater in low and high severity patches than in unburned areas. Campbell et al. (1977) found nitrate was slightly higher in burned than in unburned plots one and two years following a wildfire in southwestern ponderosa pine, although nitrate levels varied considerably among samples. Almost all nitrogen was in the form of highly soluble, thus very mobile nitrate. The period during which nitrate availability was highly variable corresponds with the wettest months on record since the fire. The Palmer Severity Drought Index indicates that the time from July to September, 2001, was a particularly wet period (NCDC 2003). We can speculate that most nitrate was probably lost by leaching during the first growing season following fire as minimal vegetative regrowth had occurred.

Fire effects on tree crowns and boles, tree mortality, and ground char increased relative to burn severity. We found all trees were killed, independent of size, in areas of high severity. Initial tree mortality was 23 % in moderately burned areas and increased to 59 % three years post-fire. Campbell et al. (1977) documented nearly 100 % mortality in severely burned and 25 % mortality in moderately burned stands following a wildfire in southwestern ponderosa pine. Fire-killed trees in moderate severity patches were ~ 17 cm DBH one year post-fire; however, larger trees take longer to die and three years post-fire, the average DBH of a fire-killed tree increased to 22 cm. Tree mortality is ongoing and cumulative mortality was greatest in areas of higher burn severity with surviving trees.

We initially found 99 % of saplings (DBH > 2.5 cm) and trees (DBH > 5 cm) experienced fire, and 30 % of saplings and 99 % of trees survived the Jasper fire in low severity patches. DBH of fire-killed trees were small (8.3 cm), but the DBH of dead trees increased to ~ 17 cm three years post-fire in low severity patches. Our data from low severity patches are similar to mortality estimates in southwestern ponderosa pine following historical surface fires. Stand replacement fires were very uncommon or non-existent in southwestern forests (Cooper 1960; White 1985; Moore et al.1999); however, small trees were often killed by small crown fire flare-ups within surface fire events (Cooper 1960). Tree mortality is ongoing and increased to 16 % in areas of low burn severity three years post-fire.

Fire alters light and seedbed conditions which can vary within burned areas, depending on the severity and pattern of the fire. Consumption of the forest floor is an important determinant of post-fire conditions because it controls the amount and distribution of good seedbed conditions. Stand structure was least changed in low severity patches as fire killed only the smallest trees and minimally scorched needles on lower branches. Forest floor litter depths have not changed significantly during the three years post-fire due to minimal canopy scorching and subsequent needle loss. Sub-canopy light penetration in low severity patches was not initially different from unburned stands due to minimal canopy disruption and tree mortality. Basal area reductions increased to 14 % three years post-fire; however, light penetration was not different from unburned stands.

Structural changes were more prominent in moderate severity patches as initial fire effects were more extensive, killing small trees and scorching the canopies and boles of larger trees. Basal area was initially reduced by16 %, and as larger trees died over time, losses totaled 46 % in moderate severity areas. Similarly, basal areas reductions were ~ 47 % in moderately burned ponderosa pine stands in AZ (Campbell et al. 1977). Forest floor litter depths were reduced by ~ 60 % in moderately burned stands compared to unburned stands. However, deposition of scorched needles was highest in moderate severity areas with a high degree of canopy scorch. Litter cover was reduced by 59 % and exposed soil increased by 80 % in areas of moderate severity following a wildfire in ponderosa pine (Campbell et al. 1977). Canopy disruption was substantial in moderate severity patches following the Jasper fire and resulted in almost twice the amount of full sunlight hitting the forest floor as in unburned stands.

Seedling regeneration is generally prolific in the Black Hills, although post-fire years have been unusually dry. Seed production was variable in areas of different fire severity, and lower in burned areas than in unburned areas. Low seed production coupled with high seed predation rates likely explain much of the variability we observed in seedling regeneration in the first three years post-fire. Given the annual local variation in seed crops (Boldt and Van Deusen 1974), we expect that successful regeneration will occur when normal moisture conditions and a good cone crop coincide.

Overstory densities ranging from 0 to 14 $m^2 ha^{-1}$ are desirable for successful regeneration of ponderosa pine seedlings in the Black Hills, although the species' intermediate shade tolerance allows for regeneration in forest canopy gaps and in full sunlight (Shepperd and Battaglia 2002). Overstory mortality was minimal in low severity patches, and basal areas were reduced to ~ 20 $m^2 ha^{-1}$ in areas of low severity. It is likely that regeneration occurring in low severity patches will have limited opportunities to emerge into the canopy due to competition from existing mature trees. In moderate severity areas, significant overstory mortality has occurred and basal areas were reduced to 12 $m^2 ha^{-1}$. By creating openings in the canopy in the midst of surviving seed producing individuals, moderate burn severity creates establishment and survival opportunities for regeneration. We have observed essentially no regeneration in high severity patches. Interior areas of high severity patches are limited by seed source and high predation rates.

Ponderosa pine is a heavy-seeded conifer, and maximum effective seed dispersal distance is estimated to be within ~ 1 to 1.5 times parent tree height (Boldt and Van Deusen 1974; Shepperd and Battaglia 2002). In contrast, lodegepole pine seeds are light, wind-dispersed, and often serotinous. Contrary to their expectations, Turner et al. (1997) found higher lodgepole pine seedling densities in smaller patches of non-crown fire; however, lodgepole pine cover was greatest in patches of crown fire. Crown fire may consume cones while less severe fire may open serotinous cones (Johnson and Gutsell 1993; Turner et al. 1997), and trees establishing in less severely burned areas eventually provided the seed source for stand regeneration in large patches of crown fire following the Yellowstone fires (Turner et al. 1997). Seedling cover was higher in large crown fire patches due to increased light availability and reduced competition. Following the Jasper fire, we determined ~ 55 % of the burned landscape was greater than the effective dispersal distance for ponderosa pine. In the peripheral areas of large patches of crown fire, we expect that a dense even-aged cohort may establish when seed crop and climatic conditions conducive to seed germination occur. Areas beyond the effective seed dispersal range may revegetate as shrub communities that persist without significant tree cover for a long time.

Our data clearly show that even large fires exhibiting extreme fire behavior can leave a heterogeneous landscape pattern of burn severity. New post-fire cohort formation was related to burn severity and was detectable within a relatively fine scale matrix of surviving trees in areas of surface and mixed-mode fire behavior. New cohort formation within a single fire can occur in a variety of ways dependent on overstory mortality, soil effects, and seed source availability. Areas of low severity surface fire retain viable seed sources and experience minimal disturbance to the forest floor, but regeneration has limited opportunities to persist because of canopy density. Areas of moderate burn severity are not limited by seed source availability, but often experience extensive disturbance to the forest floor and significant canopy reduction. As a result, we expect persistent regeneration in these areas and the formation of multi-cohort stands over time. Regeneration in areas of high- severity fire is dependent on distance from seed source, severity of ground effects, and regional climate or local weather conditions. We can speculate that even-aged stands will develop in these areas if prolific regeneration occurs or that regeneration will be limited in interior areas due to lack of seed source.

The practical application of much of this ecological information addresses three main points. First of all, our work suggests that immediate post-fire assessments can be misleading. The post-fire environment will change greatly within one year, some aspects of which may be predictable while others may be related to local and regional climate. Secondly, in general, recovery is more rapid in less severely burned areas. Fire effects in areas of different severity were initially quite different; however, recovery following mixed- severity fires is strongly influenced by vegetative survival. Lastly, patch size exerts a strong influence on post-fire landscape heterogeneity and rates of recovery. Post-fire vegetation dynamics may not follow the same trajectory and a cover type conversion from forests to shrubs or meadows is likely in some extensive areas of high-severity fire. Recovery following this mixed- severity fire has been more rapid than observed in other large fires with extensive areas of high severity for two reasons. Severely burned areas that are great distances from potential tree seed sources are limited on the Jasper landscape due to the spatial arrangement of low, moderate, and high severity patches. And within these patches, many species survived to produce seed or to resprout from belowground plant parts.

This study of the Jasper fire has shown that understanding fire effects on overstory, understory, and forest floor communities may facilitate identification of areas likely to develop vegetation structure different from prefire conditions. We believe that identification of desirable attributes of fire behavior and positive post-fire effects may improve restoration strategies. For example, recognition of initial fire effects likely to result in tree death may facilitate selection of which trees to salvage harvest or leave as potential seed sources. In some areas, reforestation or seeding are probably unnecessary and could interfere with natural successional dynamics. For example, efforts to re-establish grass species to provide forage may not be necessary in less severely burned areas, as grass cover exceeds pre-burn levels within three years post-fire. From a management perspective, low rates of recovery may indicate areas that require immediate attention or are highly vulnerable to displacement of native flora by invasive nonnative species. Although, if a cover type conversion from ponderosa pine to shrub-dominated communities is desirable, then large patches of high severity may lend themselves to this objective. Lastly, we believe our data shows that longer interval, large-scale fire events may be critical in maintaining landscape heterogeneity and diversity. Openings in a previously dense, closed-canopy forest may represent a desirable departure from pre-fire conditions and a return of some attributes of historical landscape function. Therefore, management and restoration efforts need to recognize the importance of large events in creating structural, age, and species diversity across the landscape. Mixed- severity fires like the Jasper fire leave a lasting imprint on the landscape and may explain how landscape structure was maintained in historical Black Hills forests.

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Table 3.1. Description of criteria used to identify areas of different burn severity after the Jasper fire.

Burn severity Class	**Low**	**Moderate**	**High**
% of Fire Area classified by GIS-based Severity Map	25	48	27
Type	Surface	Mixed surface & crown	Crown
Description	Needles green or scorched; Litter scorched or consumed; Duff intact; Mineral soil unaltered. Residual downed woody material partially scorched.	Needles scorched, but not consumed; litter & duff largely consumed. Soil covered by dead leaves fallen from the canopy. Mineral soil not visibly altered. Residual downed woody material deeply charred.	Needles of canopy trees completely consumed by fire; soil organic layer almost entirely consumed. Soil is bare with no litter. Mineral soil reddish or orange. Deep charring of soil. Downed woody material in a charcoal-like state.
Initial Aboveground Mortality	Patchiness in Understory	Patchiness in Understory & Overstory	Understory & extensive Overstory
Distance to Live edge	0 m	< 10 m	> 30 m

Table 3.2. **Summary of experimental design in the Jasper fire.**

Number	**Type**	**Description**
3	Study Areas	North, Central, and South
4	Fire Severity Classes	Unburned, Low, Moderate, and High
3	Replicates	Site 1, 2, and 3
36	**Study Sites**	

Table 3.3. Description of stand structures in burn classes in the Jasper fire area.

	Average Stand Diameter (SE) (cm)	**Tree Height (SE) (m)**	**Density (SE) (trees ha^{-1})**	**Basal Area (SE) ($m^2 ha^{-1}$)**
Unburned	21.7 (1.1)	12.5 (0.6)	727.2 (108.6)	24.9 (1.0)
Low	22.3 (1.38)	11.8 (0.7)	665.4 (136.7)	23.2 (2.5)
Moderate	23.9 (0.6)	13.2 (0.3)	520.1(59.2)	22.8 (2.1)
High	20.7 (0.6)	13.1 (0.2)	825.9 (67.7)	26.4 (1.2)
Pr > F	0.0787	0.2648	0.1189	0.3496

**** denotes significance ($P < 0.05$)**

Table 3.4. Direct fire effects measured on the boles and in crowns of trees after the Jasper fire.

Burn Severity	Crown Scorch (SE) (%)	Crown Consumption (SE) (%)	Bole Scorch (SE) (%)	Basal Scorch (SE) (%)	Basal Char (SE) (%)	Bole Scorch at 1m (SE) (%)
Low	19.5 (3.3)	0.1 (0.1)	15.2 (2.1)	80.2 (4.1)	8.7 (3.6)	35.3 (7.6)
Moderate	69.7 (4.3)	4.9 (2.2)	41.9 (3.2)	79.3 (6.2)	19.2 (6.2)	87.1 (2.6)
High	8.8 (7.3)	90.6 (7.3)	99.7 (0.2)	48.2 (9.3)	51.8 (9.3)	99.9 0.1)
Pr > F	0.0001 **	0.0001 **	0.0001 **	0.0001 **	0.0001 **	0.0001 **

** denotes significance ($P < 0.05$)

Table 3.5. Tree size of surviving and fire-killed trees in the Jasper fire area.

	Pre-fire Live (SE) (cm)	Post-fire Live (SE) (cm)	Dead in '01 (SE) (cm)	Dead in '02 (SE) (cm)	Dead in '03 (SE) (cm)
Unburned	21.7 (1.1)	21.7 (1.1)			
Low	22.3 (1.4)	22.3 (1.4)	8.3 (0.9)	13.2 (2.3)	16.7 (2.0)
Moderate	23.9 (0.6)	25.2 (0.8)	16.9 (2.4)	18.5 (1.9)	21.4 (1.1)
High	20.7 (0.6)	-----	20.7 (0.6)	-----	-----
Pr > F	0.0787	0.2597	0.0001 **	0.0002 **	0.0030 **

**** denotes significance (P < 0.01)**

Table 3.6. Total vegetation cover by species cover type and species richness during the first three years following the Jasper fire.

May 2001	Total Veg Cover (%)	Grass Cover (%)	Forb Cover (%)	Shrub Cover (%)	Species Richness
Unburned	37.5 (0.6)	7.2 (2.4)	7.6 (2.0)	21.6 (4.0)	43
Low	12.7 (0.3)	4.6 (1.0)	6.5 (2.3)	1.4 (0.6)	40
Moderate	6.3 (0.3)	1.6 (0.5)	4.4 (2.1)	0.3 (0.1)	22
High	2.4 (0.1)	0.4 (0.1)	1.3 (0.2)	0.6 (0.2)	26

August 2001	Total Veg Cover (%)	Grass Cover (%)	Forb Cover (%)	Shrub Cover (%)	Species Richness
Unburned					
Low	24.6 (0.4)	8.0 (2.2)	11.4 (2.4)	5.0 (1.3)	43
Moderate	17.7 (0.3)	3.3 (0.8)	10.3 (2.9)	4.1 (1.4)	44
High	10.6 (0.2)	1.1 (0.2)	6.3 (1.5)	3.2 (1.1)	40

August 2002	Total Veg Cover (%)	Grass Cover (%)	Forb Cover (%)	Shrub Cover (%)	Species Richness
Unburned	51.4 (0.5)	12.2 (2.2)	13.5 (2.7)	24.6 (4.4)	58
Low	47.9 (0.4)	18.7 (2.2)	16.2 (2.9)	12.7 (3.5)	68
Moderate	41.0 (0.3)	9.1 (1.6)	24.0 (2.8)	7.7 (2.0)	53
High	37.4 (0.2)	3.2 (0.6)	23.2 (2.5)	11.0 (2.9)	58

August 2003	Total Veg Cover (%)	Grass Cover (%)	Forb Cover (%)	Shrub Cover (%)	Species Richness
Unburned	52.3 (0.7)	11.8 (2.7)	15.1 (2.6)	23.3 (4.5)	63
Low	49.2 (0.6)	15.3 (2.5)	21.1 (4.2)	9.3 (2.5)	68
Moderate	65.6 (0.6)	13.0 (2.4)	41.0 (2.2)	8.6 (2.4)	62
High	57.6 (0.2)	6.5 (1.1)	34.8 (3.2)	16.3 (3.6)	38

Table 3.7. Regeneration from root stock after the Jasper fire.

Burn Severity	# of individuals	% of species regenerating from surviving root stock		
		Grass	Forb	Shrub
Low	1560	85.1(2.5)	65.1 (3.3)	86.7 (4.5)
Moderate	1180	89.0 (2.8)	49.5 (4.0)	91.8 (2.5)
High	1200	74.7 (6.0)	45.6 (3.6)	81.9 (3.7)
Pr > F		0.0439 **	0.0003 **	0.1775

** denotes significance $P < 0.05$

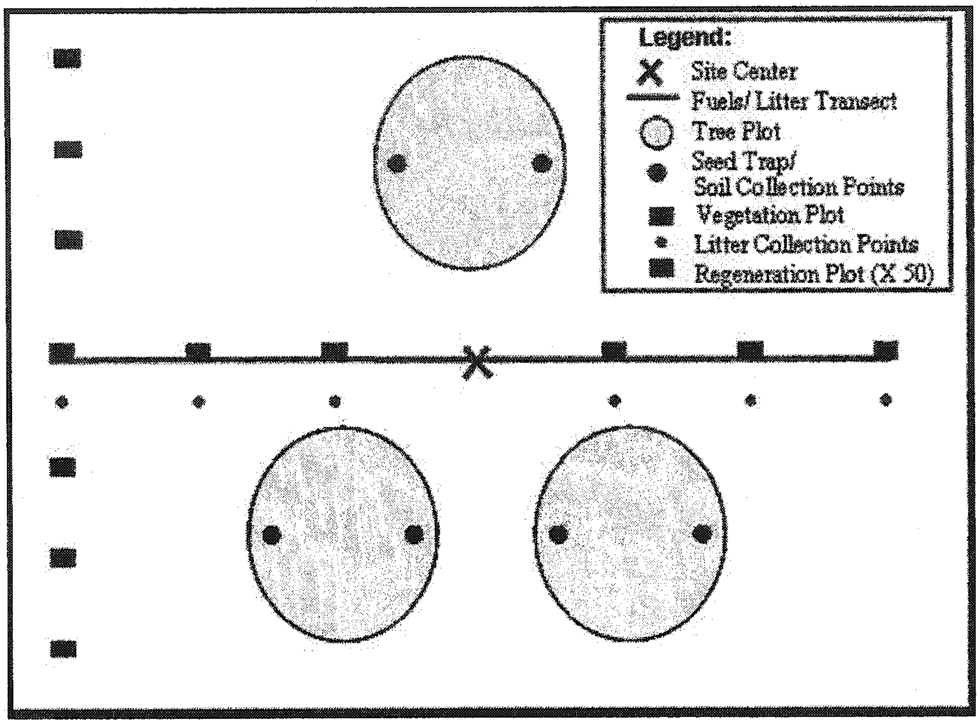

Figure 3.1. Schematic of study site layout in the Jasper fire.

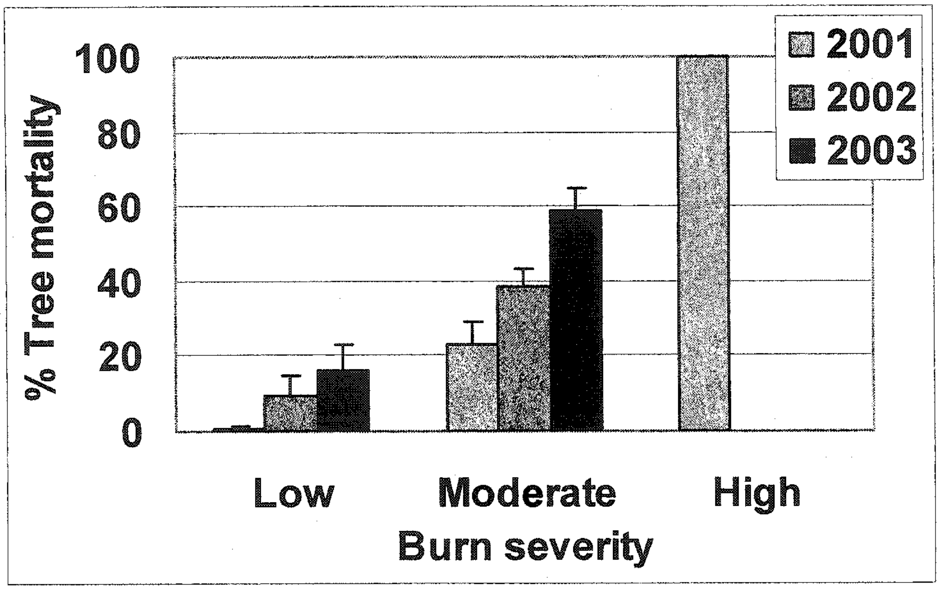

Figure 3.2. Tree mortality by burn severity after the Jasper fire.

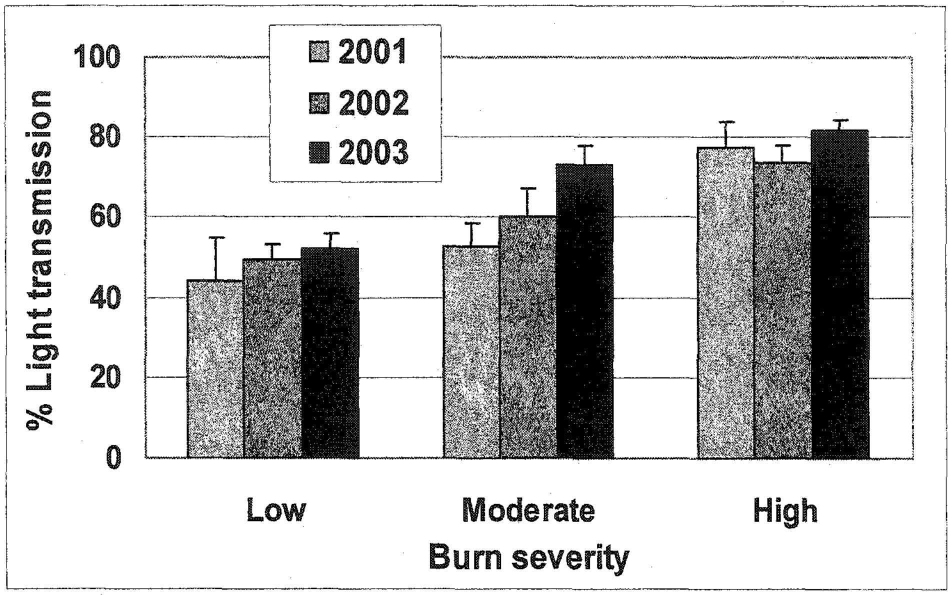

Figure 3.3. Light transmission by burn severity after the Jasper fire.

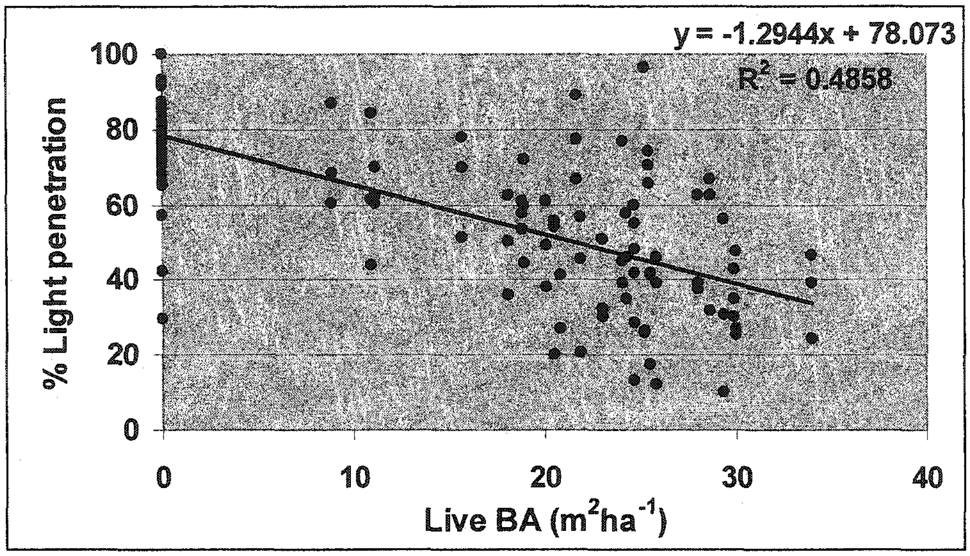

Figure 3.4. Light vs. live BA after the Jasper fire.

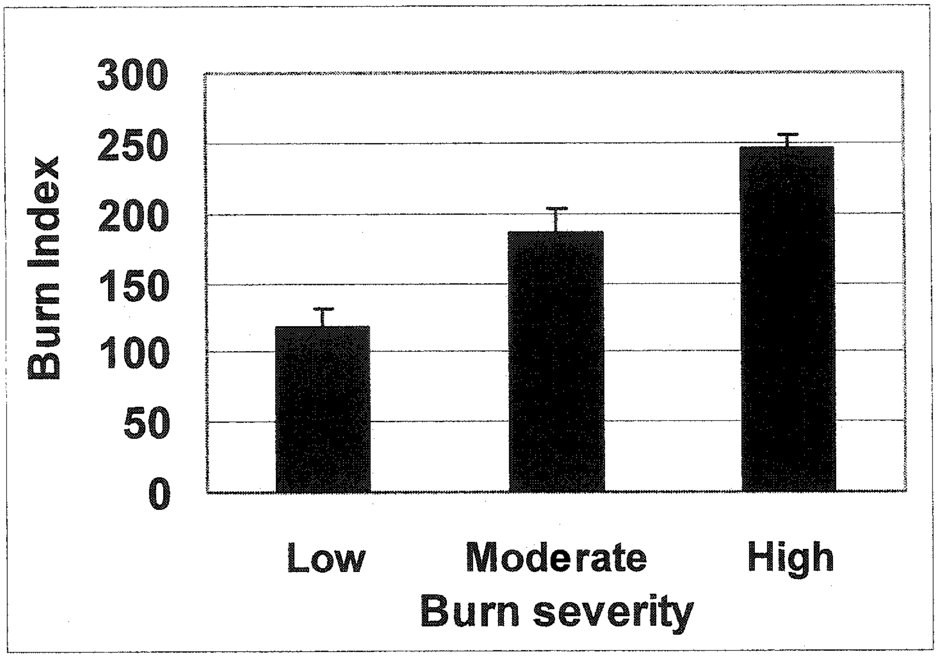

Figure 3.5. Burn index of the forest floor immediately after the Jasper fire.

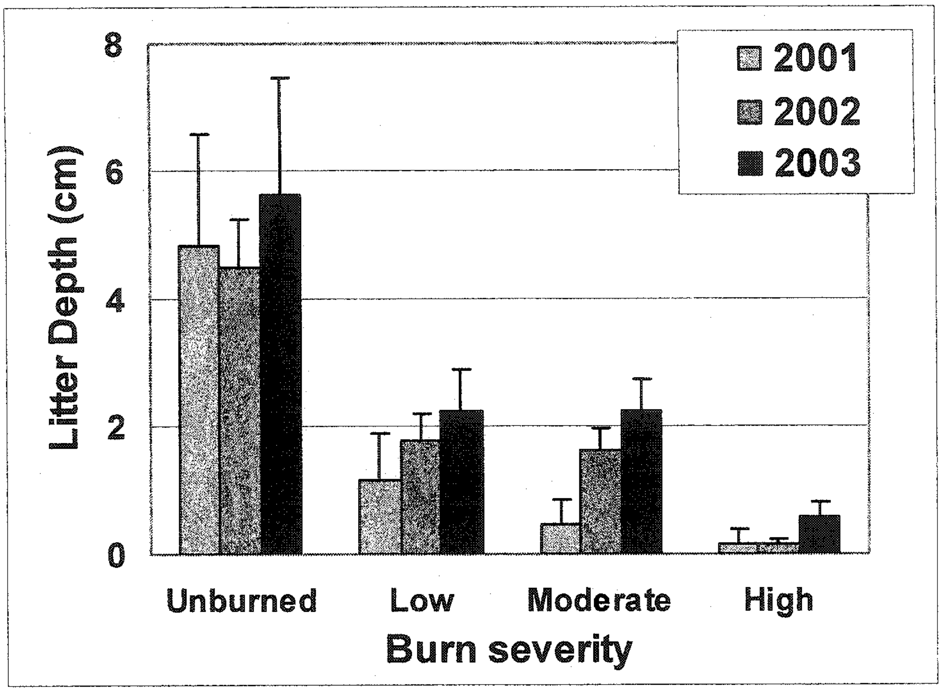

Figure 3.6. Litter depth after the Jasper fire.

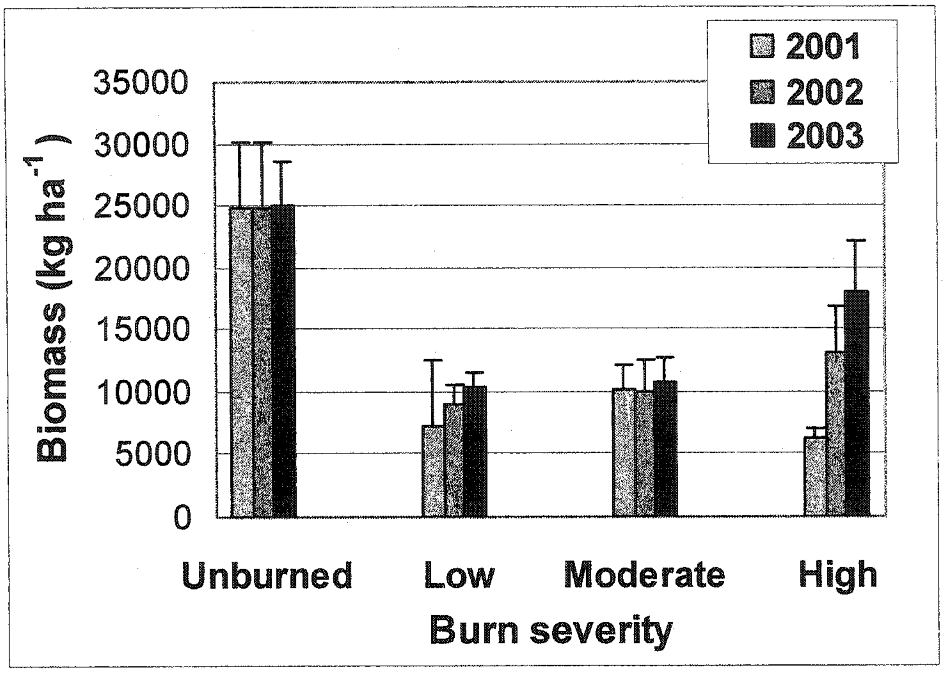

Figure 3.7. Downed woody material by burn severity after the Jasper fire.

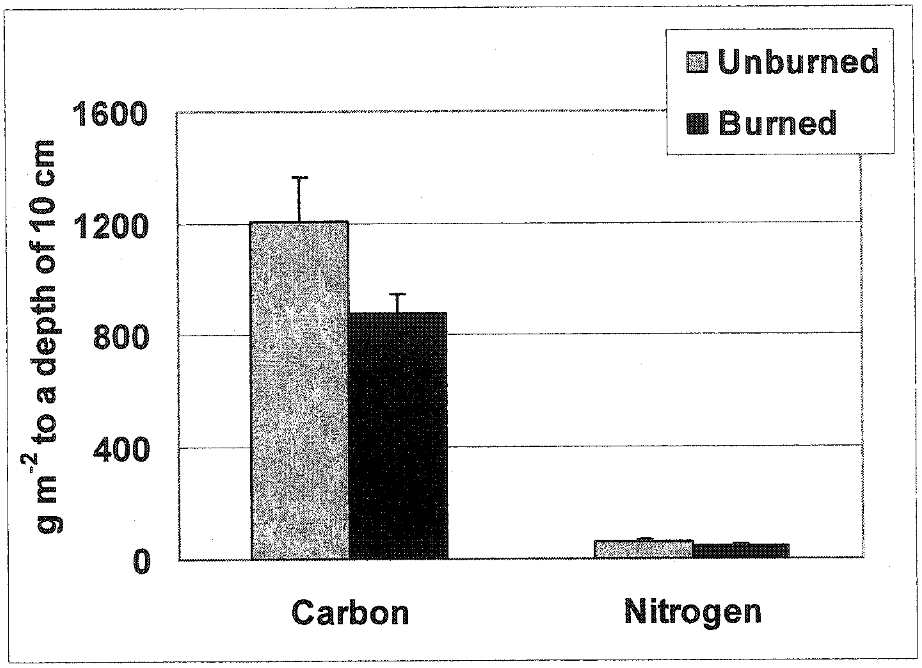

Figure 3.8. The two-year average of total soil carbon and total soil nitrogen after the Jasper fire.

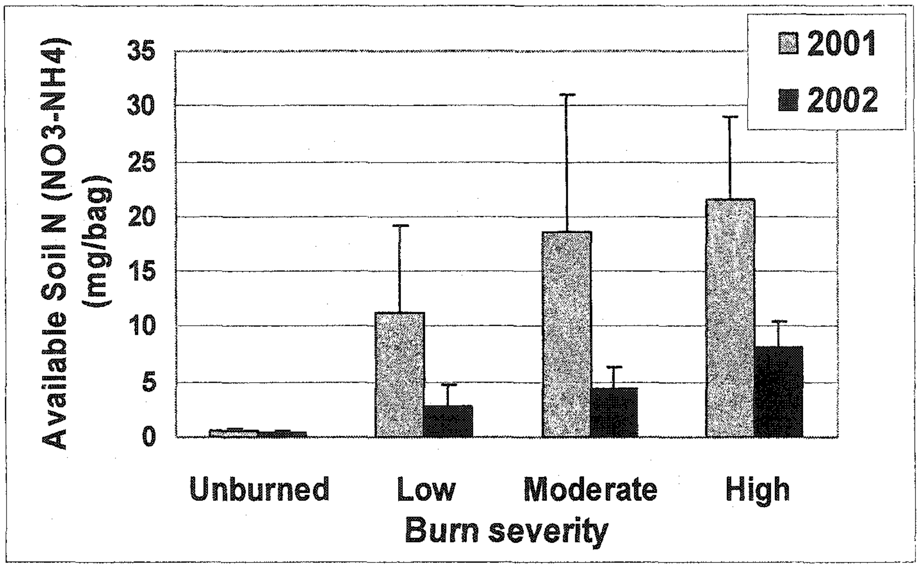

Figure 3.9. Available soil nitrogen by burn severity after the Jasper fire.

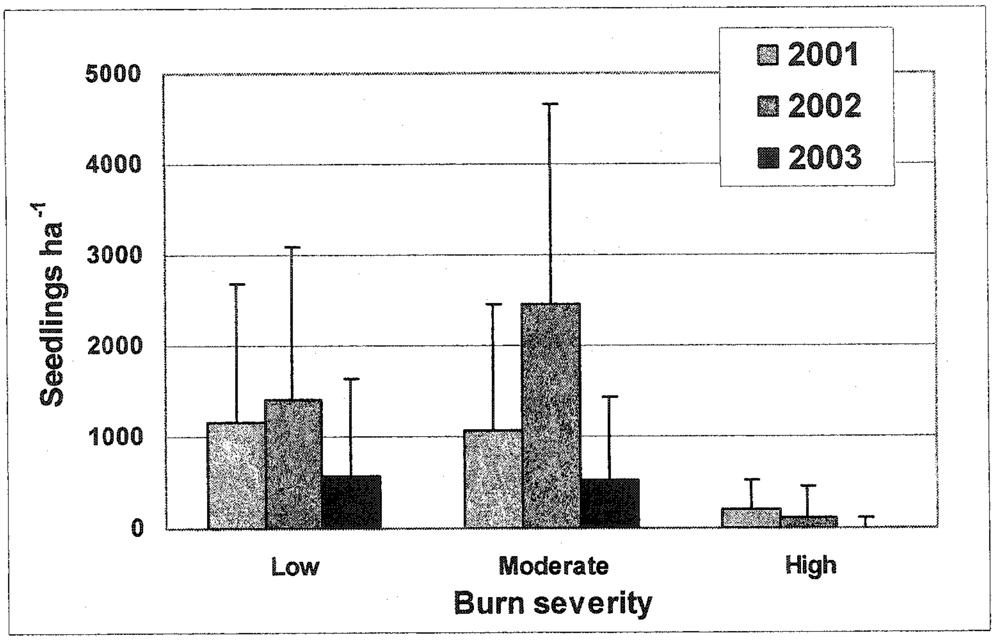

Figure 3.10. Ponderosa pine seedling regeneration after the Jasper fire.

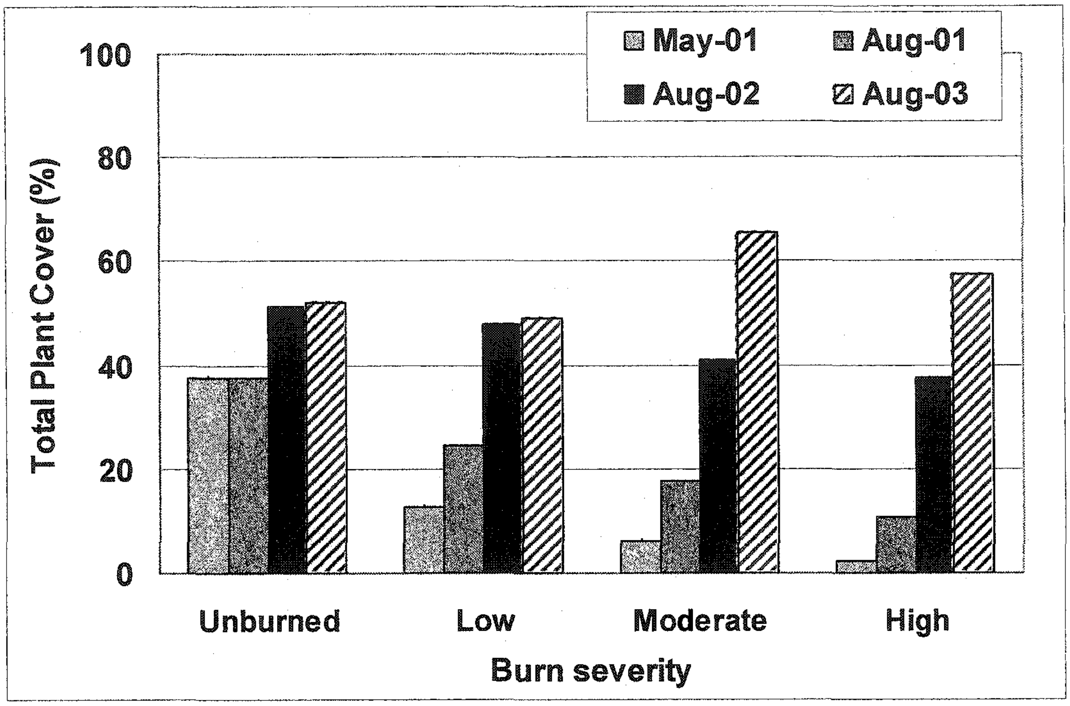

Figure 3.11. Plant cover after the Jasper fire.

IV. FIRE HISTORY EVIDENCE FOLLOWING THE 2000 JASPER FIRE, BLACK HILLS, SD

ABSTRACT

Fire histories in ponderosa pine *(Pinus ponderosa var scopulorum)* forests are reconstructed from fire scar and tree origin information. Fire frequency, severity, and size are inferred from dates of fire occurrence as recorded as scars on individual trees and from cohort origin and structure. However, little is known about rates of fire scar formation in relation to burn severity and stand conditions, and critics have proposed a modern calibration to validate sampling and interpretation of fire history evidence. We examined tree mortality, incipient fire scar formation and ponderosa pine regeneration in patches of low, moderate, and high burn severity 2-3 years following the large (~34,000 ha) Jasper fire of 2000 in the Black Hills of SD. Two years post-fire, tree mortality was ~ 6, 24 and 100 % in low, moderate and high burn severity. Three years post-fire, tree mortality had increased to ~ 21 and 52 % in areas of low and moderate burn severity. Two years post-fire, we examined ~ 2100 live trees for evidence of dead cambium within low and moderate severity patches. Dead cambium on a significant portion of tree circumference in a tree with live cambium and a vigorous crown was taken as evidence of incipient fire scar formation. Dead cambium was detected on ~ 24 and 44 % of surviving trees in low and moderate burn severity patches. Regeneration densities were ~

531, 796, and 11 seedlings ha^{-1} in low, moderate, and high severity patches two years post-fire. Three years post-fire, regeneration densities were ~ 612 and 450 seedlings ha^{-1} in low and moderate severity patches, and we observed no regeneration in high severity patches. Tree-dominated cover may not return to the interior of large patches where the distance to seed source exceeds ponderosa pine seed dispersal distance for a long time. The pattern of future fire-scarred trees and post-fire cohorts that resulted from the Jasper fire is indicative of a mixed- severity fire regime consistent with fire history reconstructions in Black Hills ponderosa pine forests.

INTRODUCTION

Forest structure and fire behavior are both cause and consequence of the landscape pattern following large wildfires. Fire-history researchers examine historical evidence of fires to better understand tree densities and stand conditions that influenced and were influenced by fire, as restoration of these conditions is increasingly a goal of management (Fule et al. 1997; Covington 2000; Baker and Ehle 2001). The role of fire in western forests has been largely inferred from examination of basal fire scars (Weaver 1951; Arno and Sneck 1977; Dieterich and Swetnam 1984; Baisan and Swetnam 1990) and stand structure and establishment patterns (Cooper 1960; White 1985; Fule et al. 1997). Inference has been drawn from work done to provide a physiological explanation and physical description of how fire kills cambium on trees of various sizes under simulated or controlled conditions (Fahnestock and Hare 1964; Vines 1968; Gill 1974; Gutsell and Johnson 1996); yet less emphasis has been placed on the relationship between burn severity and fire scar formation and its ecological interpretation. Critics have proposed a modern calibration to validate sampling and interpretation of fire history evidence (McBride 1983; Johnson and Gutsell 1994; Minnich et al. 2000; Baker and Ehle 2001), and, to this end, Fulé et al. (2003) found strong correspondence between fire-scar data and fire-record data for all but very small fires, supporting the reliability of the fire-scar approach for reconstructing fire patterns. In this paper, we explore relationships between commonly studied evidences of historical fire occurrence and burn severity and speculate concerning the interpretation of observed patterns following a single, recent Black Hills fire.

Historical fire regimes in ponderosa pine *(Pinus ponderosa var scopulorum)* forests in the Black Hills have been reconstructed from fire scar (Brown and Sieg 1996, 1999; Brown et al. 2000), tree origin information (McAdams 1995), and photos and documentation recorded by early explorers (Shinneman and Baker 1997; Grafe and Horsted 2002). There are two alternate ideas about the historical fire regime and resulting vegetation in interior pine forests of the Black Hills. The first is a fire regime dominated almost entirely by low to moderate severity (not stand- replacing) fire. Dendrochronological evidence suggests that late-season surface fires burned every 20-25 years (fire interval range 1-45 yrs) (Brown and Sieg 1996). Methodological limitations prevent drawing any conclusions regarding the spatial extent of these fires except to suggest that topographically imposed fire breaks exist. In the southern Black Hills, a low- severity fire regime would maintain an all-aged forest structure as frequent, periodic burning would reduce dense regeneration, maintaining classic open, park-like structure associated with southwestern ponderosa pine systems, but with longer fire-free intervals than typical of the Southwest. The second idea is that of Shinneman and Baker (1997), who interpret vegetation descriptions within early explorer's reports as evidence of infrequent, extensive, stand-replacing fires. These high- severity fires would create even-aged, dense patches of regeneration and subsequent relatively dense, closed-canopy forests. Shinnemann and Baker (1997) suggest that this type of disturbance dynamic may dominate the cooler, moister, central and northern Black Hills, and that a surface fire interpretation may be appropriate for the warmer and drier southern Black Hills. Variability in Black Hills fire regimes has been related to climate, elevation, topography, and fuel loads (Brown et al. 2000; Shepperd and Battaglia 2002); however, discrepancy in interpretation may be attributed to methodological approaches and a lack of modern calibration.

Early explorers described effects, extent and residual pattern of large historical wildfires (Ludlow 1875; Newton and Jenny 1880; Graves 1899; Gartner and Thompson 1972; Raventon 1994; Dodge 1996); however, until now, there has been limited opportunity to conduct research immediately following a large wildfire in the Black Hills. Large fires may have occurred infrequently in this landscape. In the 1899 forest inventory survey report, H.S. Graves wrote that patches of forest ~100 years old could be found everywhere in the Black Hills. Specifically in the geographic region known as the Limestone Plateau, Graves referred to the occurrence of severe fires in 1888 and 1890, badly burned areas of compacted sod that appeared to limit pine regeneration, and patches of timber mortality on the scale of several hundred acres. He described multiple cohort stands with older, badly scarred, decadent trees, short in stature with full crowns that appear to have regenerated in very open conditions following a large fire, as well as younger, ~ 100 years old trees, that appeared to have regenerated in forest canopy gaps (Graves 1899). Several large fires have also been documented in the post-European settlement era. In the1890's two large fires burned ~31000 ha in the northern Black Hills, and in the 1930's the Rochford and McVey Fires burned ~17000 ha on the Limestone Plateau. Both of the latter fires were described as wind-driven and fatal to nearly all the standing timber (USDA 1948).

In nine days in late summer of 2000, the Jasper Fire burned an area of ~33,800 ha or ~7% of the forest lands of the Black Hills National Forest, SD. This was the largest recorded fire in the history of the Black Hills. The Jasper Fire burned under a variety of fuel and weather conditions creating a mosaic of vegetative mortality in patches of varying size and extent. Examination of fire evidence in areas of known burn severity is the first step in providing a modern calibration to test how the fire-scar record should be interpreted to reconstruct past fire events. The purpose of this study was to determine if it is possible to detect incipient fire scar formation, and, if so, to test the rate of fire scar formation and regeneration recovery in areas of known burn severity. In the 1988 Yellowstone fires, smaller patches were often more heterogeneous in fire effects and overall less severely burned, whereas larger patches were more homogenous in effects and more severely burned (Turner et al. 1994). For this reason, we expected that patterns of fire history evidence in the Jasper fire would differ in low, moderate, and high severity patches. We expected low burn severity patches would be small relative to high burn severity patches and would have many well-distributed fire scars originating after the 2000 fire. We expected that seedling regeneration would occur, but would not persist due to high canopy cover and low light environments. We expected that patches of moderate burn severity would be larger and contain many surviving trees with scars dating to 2000. Seedling regeneration would be sparse and scattered, but would have a higher likelihood of emergence into the canopy. Patches of high burn severity would be the most extensive and contain no scars as no trees survived the 2000 fire. We expected dense seedling regeneration would form an even-aged post-fire cohort in high severity patches. An understanding of the landscape pattern created by this large, mixed- severity wildfire allowed us to retrospectively evaluate important lines of historical evidence.

To provide a quantitative assessment of the reliability of fire scar sampling in reconstruction of historical fire regimes, we calculated rates of scarring in areas of different burn severity, and we related tree size, bark thickness, and pre-existing scar presence to likelihood of new scar formation. In four early studies, rates of fire scar formation in ponderosa pine ranged from 22–51 % following surface fire (Lachmund 1921, 1923; Show and Kotok 1924; Morris and Mowat 1958). We expected that surviving trees in areas of higher burn severity would experience greater cambial death, both on individual stems and proportionally within the stand. While more likely to survive in general, larger trees are less likely to form a scar due to thicker bark with greater insulative properties (Fahnestock and Hare 1964; Vines 1968). We expected a lower incidence of cambial death on larger diameter trees with thicker bark. Several studies have shown that once a tree has scarred that it becomes more likely to scar again (Lachmund 1923, McBride 1983; Johnson and Gutsell 1994). Rates of re-scarring ranged from 71 -100 %, although pre-existing scars were probably more prevalent in these early studies (Lachmund 1923; Show and Kotok 1924). We expected trees with pre-existing scars or wounds would have a higher rate of scar formation. Comparisons of the density and distribution of fire scars on surviving trees of different sizes gave us a better understanding of how fire history evidence is formed in areas of different burn severity.

METHODS

2.1 Study Area

The Black Hills is an isolated and forested mountain range rising over 1000m above the Great Plains of western South Dakota and northeastern Wyoming (Boldt and Van Deusen 1974; Shepperd and Battaglia 2002). As the easternmost extension of the Rocky Mountains, the Black Hills was formed by regional uplift ~35 to 65 million years ago. This uplift produced an elliptical dome with an older crystalline core surrounded by younger, steeply dipping sedimentary deposits (Froiland 1990). The Limestone Plateau surrounds the core and the area burned by the Jasper Fire is located on the southwestern extent of this fertile plateau. Intensively managed ponderosa pine forms the dominant vegetation matrix, but scattered aspen (*Populus tremloides*) clones and meadowland inclusions are found in the study area. Natural regeneration of pine is abundant and relatively constant due to favorable moisture conditions throughout the spring and summer (Shepperd and Battaglia 2002). Persistent harvesting over the past century, coupled with insect, disease, wind and ice-related mortality, and fire suppression, has resulted in the conversion of the old-growth pine forest to a relatively homogenous, heavily stocked, second-growth forest with a high degree of fuel build-up and continuity.

2.2 Plot Sampling

We used color infrared aerial photography and a GIS-based map of burn severity (Gould 2003) to identify sampling areas. The burn severity map was based on three visually distinguishable burn severity classes. Following fire, the appearance of vegetation, litter, duff, and upper soil horizons can be used to estimate the amount of heat radiated downward into the underlying duff and mineral soil (DeBano et al. 1998; Ryan and Noste 1985). The magnitude of the observed change depends largely on the intensity of the fire. Several aspects of burn severity can be quantified, but burn severity cannot be expressed as a single quantitative measure that relates to resource impact (DeBano et al. 1998; Robichaud et al. 2000). Therefore, we used relative magnitudes of burn severity, expressed in terms of post-wildfire appearance of vegetation, litter, and soil, to place burn severity into broadly defined, discrete classes ranging from low (surface) to moderate (mixed surface and crown) to high (crown) (Table 1).

Study areas contained a mosaic of low, moderate, and high burn severity and were not impacted by post-fire management activities. All study areas were located between latitudes 43° 41' 35" - 43° 55' 48", longitudes 103° 46' 1"- 104° 0' 47", and elevations ~1500-2100 m. All plots were permanently located with a Garmin ® GPS unit.

We measured pre-fire tree density, fire-caused mortality, incipient fire scar formation and tree regeneration densities in five ~600 ha areas within the fire perimeter. We assessed tree mortality and regeneration density in 2002-2003. Initially, we identified ten areas that met the criteria for sampling. We randomly selected one area for a pilot study. During this preliminary study, we compared the efficacy of tools and identified characteristics that facilitate the differentiation of live and dead cambium. We sampled cambium on 150 trees at 30 cm height with an increment hammer, a portable drill with a 3.2 cm steel hole-saw attachment, and a hatchet. We examined extracted or exposed cambium to determine live or dead status. We attempted to locate both live and dead phloem on the same live tree. If a tree had both live crown and live cambium then we considered it a fire survivor and a candidate for fire scarring. The detection of dead phloem on 10% or more of the circumference of a fire survivor signified the formation of an incipient fire scar. During the preliminary study, we determined that the increment hammer, drill, and hatchet all produced acceptable samples to determine cambial status, although the hatchet had the fewest disadvantages. Removal of the sample from the hammer was time-consuming and repeated strikes to the tree were often required to obtain one sample for examination. The drill also yielded a reliable sample, but drawbacks included the weight of the drill and the difficulty associated with the transport of a sufficient number of battery packs. We determined that the hatchet was the simplest, most lightweight, and most direct means by which to expose and evaluate cambium. The hatchet exposed the greatest amount of surface area for examination and was reliable. With the hatchet, virtually every strike was informative and live cambium was easily distinguishable from dead cambium. Live cambium appeared white in color and cool, wet and spongy to the touch. Dead cambium was tan-yellow in color and dry to the touch. In our pilot study, we established that it is possible to differentiate between live and dead phloem and that both can be found on the same live tree.

We selected five study areas from the remaining nine. Twenty variable radius (2.2 metric basal area factor) plots were located per severity class within the five areas for a total of 100 plots per burn severity class. We assessed tree characteristics of status (live, dead due to fire-kill, pre-fire dead) and crown vigor (Table 2) on all trees within each plot. We measured diameter and bark thickness at 1.4 m height on all live trees. On every tree containing live crown, we sampled the cambium at 30 cm height with a hatchet on the face exhibiting the most severe bole scorch. If dead phloem was detected according to the above methodology then we sampled for live phloem at a total of eight positions on the same tree. On each tree with live phloem, dead phloem, and live crown, we measured the amount of dead phloem on the bole circumference. We recorded pre-existing scars or cambial wounds separately. This methodology allows us to estimate the density of fire scars per hectare as a percentage of the survivors per burn severity.

Within every overstory plot, we surveyed post-fire pine regeneration. We recorded seedling status (live or dead) and age in three circular 3.14 m^2 plots for a total of 300 plots per low, moderate, and high burn severity class.

2.3 *Data Analysis*

We performed all summary and statistical analyses in SAS V. 8.2 (SAS Institute 2001). We compared values in an ANOVA model (PROC GLM, SAS Institute 2001). Variables were tested for significance at the 95% confidence level (alpha = 0.05).

RESULTS

Before the fire, our study sites were well-stocked, ponderosa pine stands. Average stand diameter was 24.7 cm, mean tree density was 658.2 ha^{-1}, and basal area was 27.5 m^2 ha^{-1} (Table 3). Pre-fire average stand diameter was least in the high severity class and greatest in the low severity class. Pre-fire stand density and basal area were not statistically different in areas of different burn severity ($P < 0.05$).

We examined ~3800 trees two years following fire and found 5.5, 23.8 and 100% mortality in areas of low, moderate, and high severity. Fire selectively killed smaller diameter trees in areas of low and moderate burn severity, and no trees, regardless of diameter, survived in areas of high burn severity. Average diameter of fire-killed trees was 25.2, 20.9, and 20.7 cm in low, moderate, and high severity (Table 4). Diameter of fire-killed trees in low and moderate severity areas was significantly different ($P < 0.05$). Tree mortality increased over time and three years post-fire, tree mortality was 20.8 and 51.8 % in areas of low and moderate severity (Fig. 1). Tree mortality was significantly different in areas of different burn severity and over time ($P < 0.05$).

We examined ~ 2100 live trees in areas of low and moderate severity. We found only two trees that did not appear to have been directly affected by fire. The basal circumference was entirely scorched on 31% of trees. Ninety-nine and 88% of live trees surveyed in low and moderate severity were rated as likely to survive based on assessments of crown vigor. Of trees likely to survive, 23.6 and 43.7 %, or 122.7 and 162.8 trees ha^{-1}, met the criteria for incipient fire scar formation in low and moderate severity (Fig. 2), a difference that was significant ($P < 0.05$). For the average tree that met the criteria for incipient fire scar formation, we found 34.4 and 38.1 % of the basal circumference had dead cambium in low and in moderate burn severity classes. The amount of dead cambium on surviving trees was not significantly different in areas of low and moderate severity ($P < 0.05$). There were no surviving trees in high severity areas; therefore, no candidates for fire scarring.

There were no significant differences ($P <0.05$) in tree size or bark thickness between live trees with dead cambium and those with no dead cambium (Table 5). Mean diameter was 29.5 and 28.7 cm for live trees with dead cambium in areas of low and moderate severity. Mean diameter was 28.8 and 29.1 cm for surviving trees with no dead cambium in low and moderate severity. Bark thickness was 1.5 cm for live trees with dead cambium in areas of low and moderate severity. On trees with no dead cambium, bark thickness was 1.6 and 1.5 cm in low and moderate severity. We examined rates of fire scar formation in trees with and without pre-existing scars or wounds. Approximately 10% of all live trees had a preexisting scar or wound. Thirty-eight and 62% of trees with pre-existing dead cambium experienced additional cambial death following the Jasper Fire in low and moderate classes, respectively (Table 6). Trees with pre-existing scars or wounds were ~ 1.7 times more likely to experience additional cambial mortality.

Two years post-fire, post-fire seedling regeneration densities were 530.8, 796.2, and 10.6 seedlings ha^{-1} in areas of low, moderate, and high severity. Three years post-fire, cumulative regeneration densities were 612.2 and 450.3 seedlings ha^{-1} in areas of low and moderate severity. There was no regeneration in high severity areas. Regeneration densities were not significantly different ($P < 0.05$) among areas affected by different burn severity in either year (Fig. 3).

DISCUSSION

How were patches of burn severity distributed on the landscape following the Jasper fire?

The spatial pattern of burn severity caused by a large wildfire in the Black Hills was different from those created by wildfires in other regimes. Although ~ 60 % of the total acreage burned in less than 12 hours, we found considerable variability in fire effects over a large area. Patches of low, moderate, and high burn severity were small relative to total daily area burned and relatively evenly distributed on the landscape (Lentile Dissertation Chpt. 1). In contrast, patch sizes were large (~ 3500 ha) following the Yellowstone fires, and crown fire burned 31 % or ~ 70,000 ha in these subalpine lodgepole pine (*Pinus contorta* var. *latifolia*) forests (Turner et al. 1997). High- severity fire impacted ~ 28,000 ha, roughly half of the landscape burned by the Hayman fire, CO in 2002. Small "escapes" or narrow "tree crown streets" were embedded within large patches of crown fire in these montane ponderosa pine (*Pinus ponderosa* var. *laws*) and Douglas- fir (*Pseudotsuga menzensii*) forests (Graham 2003). The proportion and patch sizes of high- severity fire were much smaller in Jasper; and rather than patches of surviving vegetation within a matrix of crown fire, a matrix of surviving vegetation was interspersed with patches of crown fire on the Jasper landscape (Lentile Dissertation Chpt. 1).

In spite of high temperatures, gusty winds and unstable atmospheric conditions that created extreme fire behavior, only 27% of the fire area burned under crown fire conditions. Patches created by high- severity fire were surprisingly small with the least amount of patch size variability and edge relative to low and moderate burn severity. All trees were killed by fire due to crown consumption in high severity patches. Almost half of the Jasper fire area was burned by moderate severity surface fire coupled with crown scorch and consumption. The size of moderate severity patches tended to be larger and to have the greatest amount of edge although both patch size and shape were highly variable One-fourth of the Jasper fire area was burned by low severity surface fire, resulting in scattered tree mortality. Low severity patches were larger, more complex in shape, and had a greater amount of edge than patches of high severity. The juxtaposition of low, moderate, and high severity patches in the Jasper fire mitigated the effects of high-severity fire by providing nearby herbaceous and tree seed sources and likely increased rates of post-fire vegetation recovery (Lentile Dissertation Chpt. 2).

What is the relationship between tree mortality, fire scar formation, and regeneration density and burn severity?

We saw a clear relationship between commonly examined lines of historical fire evidence and burn severity following the Jasper Fire. Patterns of differential tree mortality, incipient fire scar formation, and regeneration emerged in areas of different burn severity. Rates of tree mortality and fire scar formation increased along the severity gradient from low to moderate; however, in order to be a candidate for fire scarring, a tree must stay alive while sustaining some degree of cambial mortality. Thresholds exist for tree survivability, thereby limiting fire scar formation. Similarly, living trees are potential seed sources for natural regeneration, and fire effects on tree crowns may limit seed production or improve opportunities for seedling survival. In areas of complete tree mortality, new cohorts may not form for a long time because of inadequate seed source.

Tree mortality is ongoing in all areas with surviving trees. Tree mortality was ~ two times greater in moderate burn severity patches than in low severity patches three years post-fire. Cambial death was commonly observed on surviving trees in moderate severity patches, and to a lesser extent in low severity patches. All trees were killed in high- severity fire; therefore, no candidates for scarring. Regeneration was variable and limited in low and moderate severity two and three years post-fire. We found only one seedling in all regeneration surveys in high severity patches.

Fire differentially scorched tree canopies and killed trees, altering light regimes and seedling regeneration environments. We observed a 5% (1.5 $m^2 ha^{-1}$) and 24% (6.5 $m^2 ha^{-1}$) reduction in live basal area in low and moderate severity patches, respectively, two years post-fire. Minimal canopy disruption and essentially the same amount of full sunlight reached the forest floor in low severity patches as in unburned stands. Structural changes due to canopy scorch and tree mortality were more substantial in moderate severity patches and almost twice the amount of full sunlight reached the forest floor as in unburned stands (Lentile Dissertation Chpt. 2). Increased physiological stress due to the fire and subsequent droughty conditions may explain ongoing tree mortality that further reduced live basal areas to ~ 23 and 13 $m^2 ha^{-1}$ in low and moderate severity patches three years after the fire.

Overstory densities ranging from 0 to 14 $m^2 ha^{-1}$ are desirable for successful regeneration of ponderosa pine seedlings in the Black Hills, although the species' intermediate shade tolerance allows for regeneration in forest canopy gaps and in full sunlight (Shepperd and Battaglia 2002). Given the annual local variation in seed crops (Boldt and Van Deusen 1974), we expect that successful regeneration will eventually occur when normal moisture conditions and a good cone crop coincide. When these conditions are met, it is likely that regeneration occurring in low severity areas will have limited opportunities to emerge into the canopy due to competition from existing mature trees. Thus, we do not expert dense post-fire seedling cohorts in areas of low- severity fire. In moderate severity areas, however, where significant overstory mortality has occurred, but seed producing individuals also persist, we expect establishment of dense post-fire cohorts.

Following the Jasper fire, we determined ~ 55 % of the severely burned landscape was greater than the effective dispersal distance for ponderosa pine (Lentile Dissertation Chpt. 1). A dense even-aged cohort may establish in openings within the effective seed dispersal of ponderosa pine. We used 30 m as an estimate of maximum effective seed dispersal distance since ponderosa pine seeds disperse within ~ 1 to 1.5 times parent tree height (Boldt and Van Deusen 1974; Shepperd and Battaglia 2002). Areas beyond the effective seed dispersal range may revegetate as shrub communities that persist without significant tree cover for a long time.

How do rates of fire scar formation vary by burn severity and by tree characteristics?

Rates of fire scar formation that we observed following the Jasper Fire are similar to those reported by early timber managers ((Lachmund 1921, 1923; Show and Kotok 1924; Morris and Mowat 1958). We observed a higher proportion of surviving trees with cambial death in patches of moderate severity than in low severity patches. In an assessment of direct fire effects in nearby study areas, we observed ~35 and 87 % of the bole circumference at 1 m height and ~ 15 and 41 % of the entire tree height with evidence of scorch in low and moderate severity patches. We documented an increasing proportion of the basal circumference with evidence of scorch and char in areas of low and moderate severity, and a higher proportion of char in moderate severity patches (Lentile Dissertation Chpt. 2). As > 99% of all trees experienced some degree of fire, these observations in concert suggest that fire scar formation is highly influenced by burn severity.

Our results did not concur with other laboratory-controlled studies that found bigger trees less likely to scar (Fahnestock and Hare 1964; Vines 1968). While larger trees are more likely to survive in general, we observed no differences in scarred and unscarred tree size or bark thickness in our study, again suggesting a strong correspondence between burn severity and fire scar formation. Smaller trees are not likely to bear witness to the Jasper fire for two reasons. First, small trees have thin bark, low insulative properties, and increased susceptibility to complete cambial death. Secondly, small trees are more vulnerable to mortality from crown scorch (Gutsell and

Johnson 1996; Baker and Ehle 2001). Larger trees take longer to die, and we expect that mortality will continue to increase. Thus, our estimates of absolute fire scar density in areas of low and moderate severity probably overestimate future density as increased physiological stress related to drought and insect attack may further reduce tree survivorship.

Several studies have shown that once a tree has scarred that it becomes more likely to scar again (Lachmund 1923, McBride 1983; Johnson and Gutsell 1994). Although we observed relatively few pre-existing fire scars in our study, we found that trees with pre-existing scars or wounds were more likely to rescar, especially in areas of moderate severity. However, even with these increased odds, not all trees with pre-existing scars will witness the Jasper Fire.

How will future fire histories interpret the 2000 Jasper Fire?

The retrospective nature of this study allows us to postulate what we might see on the landscape in the future with respect to the kinds of evidence used to reconstruct historical fire regimes. First of all, we can expect to see single and multi-cohort patches mixed across the landscape with evidence of fire occurring in 2000. Fire scars on surviving trees and new cohort formation where tree mortality was substantial will provide this evidence on ~75% of the landscape. These areas were burned in low and moderate severity. When favorable regeneration conditions are met, we anticipate the possible formation of even-aged cohorts in openings on 10% of the landscape. These openings were created by high burn severity and are within the effective seed dispersal of ponderosa pine. We can speculate that a possible conversion from forests to non-forested cover types will occur on the remaining 15% of the landscape in interior areas of high severity patches that are in excess of effective seed dispersal for ponderosa pine. All of our predictions are consistent with reconstruction of historical fire effects in the Black Hills, i.e., that fire burned at variable severity, creating a mosaic of variable canopy mortality and post-fire seedling recruitment (Brown and Sieg 1996, 1999; Shinneman and Baker 1997).

A major issue in attempting modern calibration of historical fire regimes is that 20th century fire exclusion may have produced a more homogenous forest structure with increased tree densities and greater duff accumulations, and a concomitant increase in burn severity (Covington and Moore 1992, 1994a, 1994b). The Black Hills has not been immune to anthropogenic influence and significant changes since European settlement in landscape-scale processes and structure have occurred (Fisher et al. 1987; McAdams 1995; Brown and Sieg 1996; Shinneman and Baker 1997; Brown and Sieg 1999). However, we documented statistically significant and ecologically meaningful differences in fire scar formation and establishment of post-fire seedling cohorts in relation to burn severity. Even if larger areas may burn at higher severity today than in the past, the effects of low, moderate, and high- severity fire probably were similar in historical fires to the effects we documented in the 2000 Jasper fire.

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Table 4.1. Description of visual impacts to soil and vegetation in areas of different burn severity.

Burn Severity	Fire Type	Fire Effects
Low	Surface	Limited canopy effects; low tree mortality; most duff and litter retained with dense revegetation observed; > 70 % of forest floor covered with vegetation, duff, and/or litter
Moderate	Mixed surface & crown	Greater canopy effects and some tree mortality; vegetation and duff retained in patches; soil covered with scorched needles; 50-70 % of forest floor covered with vegetation, duff, and/or litter
High	Crown	Aboveground vegetation, litter, duff, and needles in canopy mostly consumed; extensive tree mortality; limited revegetation; > 50 % of overall area composed of rock, bare mineral soil, and/or litter with no remaining duff

Table 4.2. Classes of crown vigor.

Crown Vigor Rating	Description
1	Excellent crown vigor; no evidence of needle scorch or consumption; vigorous new growth observed
2	Moderate crown vigor; < 25% of needles scorched or consumed; vigorous new growth observed
3	Fair crown vigor; < 50% of needles scorched or consumed; new growth observed
4	Poor crown vigor; > 50% of needles scorched or consumed; new growth not observed
5	No live crown

Table 4.3. Pre-fire ponderosa pine stand conditions (n= 3800).

Burn Severity	**Average Stand Diameter (SE) (cm)**	**Density (SE) (trees ha^{-1})**	**Basal Area (SE) (m^{2}ha^{-1})**
Low	27.9 (2.4)	542.5 (152.0)	28.6 (4.2)
Moderate	25.6 (2.1)	606.3 (162.2)	27.5 (3.8)
High	20.7 (0.6)	825.9 (287.3)	26.4 (1.2)
Pr > F	0.0013 **	0.2008	0.3792

** **denotes significance ($P < 0.01$)**

Table 4.4. Tree diameter (SE) of surviving and fire- killed trees.

Burn Severity	**Post-fire Live (SE) (cm)**	**Fire-killed (SE) (cm)**
Low	28.4 (1.2)	25.2 (1.1)
Moderate	28.5 (2.0)	20.9 (1.1)
High	------	20.7 (0.6)
Pr > F	0.9281	0.0017**

**** denotes significance (P < 0.01)**

Table 4.5. Characteristics of surviving trees with and without dead cambium.

	Burn Severity	Tree Size (SE) (cm)	Bark Thickness (SE) (cm)
Live trees with dead cambium	Low	29.5 (1.1)	1.5 (0.02)
	Moderate	28.7 (1.6)	1.5 (0.1)
Live trees with no dead cambium	Low	28.8 (1.4)	1.6 (0.03)
	Moderate	29.1 (2.2)	1.5 (0.04)

Table 4.6. Demographics of previously scarred or wounded trees in the Jasper fire area.

Burn Severity	**Live trees with pre-existing scar or wound (%)**	**Rate of fire scar formation in trees with pre-existing scars or wounds (%)**
Low	9.6	38
Moderate	9.2	62

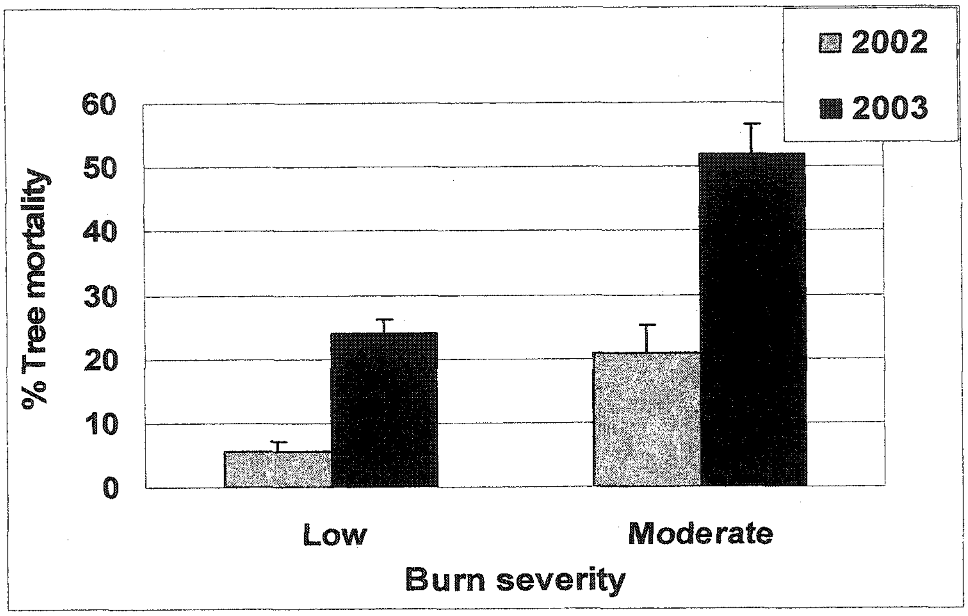

Figure 4.1. Tree mortality (SE) in areas of different burn severity (n= 2096).

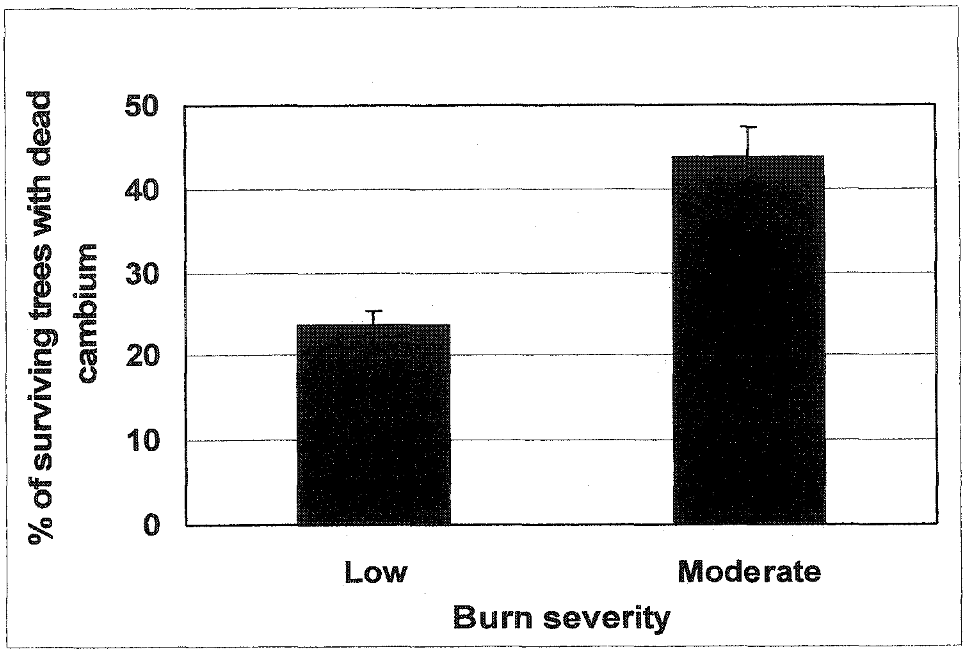

Figure 4.2. The percentage of surviving ponderosa pine trees (SE) in areas of low and moderate severity that met the criteria for incipient fire scar formation (n = 2096).

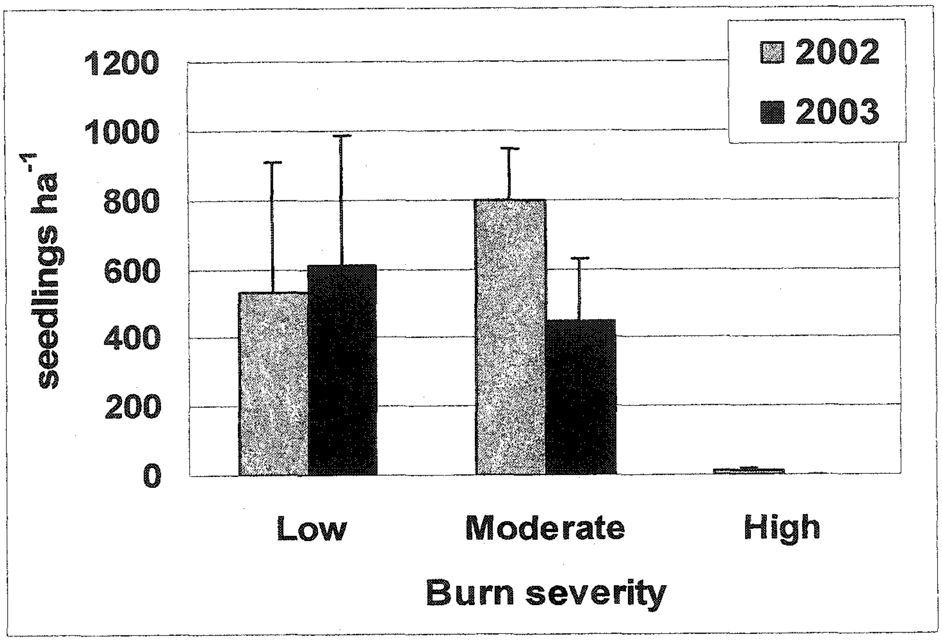

Figure 4.3. Regeneration densities (SE) in areas of low, moderate, and high burn severity.