Changes in Forest Structure After a Large, Mixed-Severity Wildfire in Ponderosa Pine Forests of the Black Hills, South Dakota, USA

Tara L. Keyser, Leigh B. Lentile, Frederick W. Smith, and Wayne D. Shepperd

Abstract: We evaluated changes in forest structure related to fire severity after a wildfire in ponderosa pine forests of the Black Hills, South Dakota, where 25% burned at low, 48% at moderate, and 27% at high severity. We compared tree mortality, fine (FWD) and coarse woody debris (CWD) and tree regeneration in areas burned under different severity. With low severity, mortality was limited to small trees (<15 cm dbh) with no reduction in basal area (BA) compared with unburned areas. FWD and CWD were 60% less than the unburned forest. With moderate severity, 100% mortality of small trees and significant large tree mortality resulted in an ~50% reduction in BA and an open stand structure dominated by a few large trees. After 5 years, FWD and CWD recovered to unburned levels. With high severity, a lack of seed source makes regeneration unlikely. After 5 years, FWD equaled levels in unburned stands and CWD loads exceeded the unburned forest by 74%. The future landscape will be a mosaic of patches with forest structures determined by developmental trajectories set in motion by different fire severities. There will be patches of fully stocked, single canopy forest, multistory forest, and persistent grass- and shrub-dominated communities. High fuel loads in moderate and high severity areas remain a concern for management as does the lack of regeneration in high severity areas. FOR. SCI. 54(3): 328–338.

Keywords: *Pinus ponderosa*, mixed-severity fire, fire severity, fire effects, postfire recovery

THE JASPER FIRE BURNED ~34,000 ha of ponderosa pine (*Pinus ponderosa* Laws.) forests in the central Black Hills of South Dakota between Aug. 24 and Sept. 9, 2000, under extreme weather conditions. Although regarded as a catastrophic event, the Jasper Fire left a complex mosaic of fire severity across the landscape, with live trees present over a significant portion of the area (US Forest Service 2000, Lentile et al. 2005, 2006). About 25% of the burned area was characterized as low, 48% as moderate, and 27% as high severity (Lentile et al. 2005). As is common in mixed-severity fires, areas of different fire severity occurred as distinct patches within close proximity to one another (Weatherspoon and Skinner 1995, Taylor and Skinner 1998, Fulé et al. 2003, Odion et al. 2004, Lentile et al. 2005). The majority (>60%) of low and moderate severity patches were >100 ha in size whereas 68% of the high severity patches were <100 ha in size (Lentile et al. 2005). Ecological recovery, including forest overstory density, tree regeneration, understory development, and accumulation of forest floor biomass will vary across patches of different fire severity. The future structure of this landscape will be the composite of thousands of distinct forest patches following specific pathways of forest development set in motion by direct fire effects. This structure will have important consequences on all aspects of forest use including timber production, fire hazard, esthetics, and wildlife habitat. In this article, we evaluate the short-term effects of a large, mixed-severity fire on forest structure in ponderosa pine forests of the Black Hills, South Dakota, and compare the processes of ecological recovery in patches burned under low, moderate, and high fire severity.

Fire behavior in ponderosa pine forests can vary from surface fire to stand-replacing, active crown fire within a single fire, significantly affecting ecological recovery (Fulé et al. 2003, Lentile et al. 2005). Immediate fire effects on forest vegetation and the forest floor are characterized as fire severity, which is often divided into three distinct categories: low, moderate, and high (Chappell and Agee 1996, Lentile et al. 2006). When surface fire occurs in ponderosa pine forests, fire severity is usually low, evidenced by little overstory tree mortality (Thomas and Agee 1986). When crown fire occurs in these systems fire severity is often high, evidenced by complete mortality of aboveground vegetation and substantial consumption of surface and canopy fuels, litter, and duff (Lentile et al. 2005). Individual fires, or fires characteristic of a fire regime, often fall into one of these two categories; however, variation in fire behavior between surface and crown fires can result in a mixed-severity fire in which partial tree mortality occurs (Agee 1993, Fulé et al. 2003, Hessburg et al. 2005).

Changes in stand structure after wildfire are the result of fire-caused tree mortality and subsequent changes in the

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Acknowledgments: This research, as part of the Jasper Fire Monitoring Project, was funded through the Black Hills National Forest Service Agreement 0203-01007 and the McIntire-Stennis program. We gratefully acknowledge our field crews who assisted in data collection and processing throughout the years and Blaine Cook of the Black Hills National Forest for continued support. We also recognize Rudy King for assistance with the statistical analysis and interpretation as well as the three anonymous reviewers whose comments and suggestions greatly improved this manuscript.

Manuscript received May 26, 2007, accepted November 30, 2007

density and size distribution of overstory trees. For ponderosa pine, tree mortality increases with increasing crown damage and (or) stem damage but decreases with increasing tree size (Stephens and Finney 2002, McHugh and Kolb 2003, Keyser et al. 2006). Consequently, in ponderosa pine systems, low fire severity often results in <20% of the prefire stand basal area (BA) being killed whereas reductions in stand density between 20 and 70% can result from moderate severity fire in these systems (Hessburg et al. 2005). The long-term changes in forest structure that result from low and moderate fire severity, in particular, may not be immediately apparent after fire as a significant proportion of mortality, especially of large trees, does not occur until 3–4 years postfire (Agee 2003, Keyser et al. 2006).

Varying rates of tree mortality associated with different levels of fire severity can affect the structure and composition of the surface woody fuel bed. After fire, there is often an immediate decrease in the abundance of both coarse woody debris (CWD) (woody biomass >7.6 cm diameter) and fine woody debris (FWD) (woody biomass <7.6 cm diameter) (Fulé and Laughlin 2006). In ponderosa pine stands that experience high tree mortality, the decrease in surface fuels is short-lived as fire-killed snags quickly transition from the canopy to the surface fuel bed (Passovoy and Fulé 2006). Little information exists regarding the temporal dynamics of fuel accumulation as it relates to fire severity. However, Chambers and Mast (2005) reported that 7 years after severe crown fire in northern Arizona, 41% of all fire-killed ponderosa pine trees had fallen compared with only 26% in an unburned plot, providing evidence that fire-killed snags fall more rapidly than unburned snags. Given the rapid fall-rate of fire killed-snags, as fire severity and, consequently, fire-caused tree mortality increases, the rate of fuel accumulation should also be expected to increase. Differential rates of fuel accumulation within patches affected by low, moderate, and high fire severity would result in a spatially complex fuel bed with varying levels of potential fire behavior (DeBano et al. 1998) in low, moderate, and high severity patches. The production of a heterogeneous fuel bed is of particular interest to land managers after wildfire because of current fuels reduction efforts and the potential for a reburn.

Fire severity, patch size, and overstory mortality interact to influence postfire seed availability, regeneration, and recruitment of forest tree species and, consequently, future forest structure and age distribution across the landscape (Taylor and Skinner 1998, Greene et al. 1999, 2005). In the Black Hills, background regeneration rates are naturally high owing to adequate moisture during the growing season (Shepperd and Battaglia 2002) and abundant seed crops every 2–5 years (Boldt and Van Deusen 1974). Conditions most conducive to the germination and establishment of ponderosa pine, however, include areas of exposed mineral soil (Harrington and Kelsey 1979) and open growing conditions (0–14 m^2/ha) (Shepperd and Battaglia 2002). Low severity fire can effectively reduce litter and duff layers (Waltz et al. 2003), thereby improving seedbed quality; however, minor amounts of overstory mortality associated with low severity fire (e.g., Agee 2003) may not promote recruitment of mid-tolerant ponderosa pine seedlings. Instead, recruitment and overstory development of seedlings may be limited to patches of moderate severity fire in which greater BA reduction results in increased light availability (Hale 2003). As the distance from the live edge increases, seedling density decreases (Greene and Johnson 2000, Bonnet et al. 2005). As a consequence, in ponderosa pine stands that experience high fire severity (e.g., 100% mortality), patch size, and proximity to a viable seed source limit regeneration (Lentile et al. 2005) as opposed to seedbed and light conditions. For example, 28 years after a stand-replacing fire in ponderosa pine forests of the Southwest, Savage and Mast (2005) reported that up to 50% of the 6,180 ha burned were converted to meadow with ponderosa pine regeneration limited to edges of the burn where a live seed source remained.

The Jasper Fire and the subsequent postfire recovery processes have provided a unique opportunity to observe how postfire stand dynamics vary in relation to fire severity. In this study, we evaluated 5 years of change in overstory vegetation, tree regeneration, forest floor, and soil to better understand the effects of a mixed-severity wildfire in heavily managed, ponderosa pine forests of the Black Hills. Specifically, we evaluated the influence that fire severity and time had on postfire overstory structure, forest floor structure, surface woody fuel loadings, postfire regeneration, and nitrogen availability. The results and interpretation of this study will provide land managers with scientifically based information regarding the short- and potential long-term changes in forest structure, which will aid in the development and modification of postfire planning objectives.

Methods

Study Area

The study area was located within the Jasper Fire perimeter in the Black Hills National Forest, South Dakota, USA (latitudes between 43°42′ and 43°57′ and longitudes between 103°46′ and 104°1′). The Black Hills are an isolated, forested uplift that rise ~900–1,200 m above the surrounding Great Plains in southwestern South Dakota and northeastern Wyoming (Hoffman and Alexander 1987, Froiland 1990). The climate is continental with cold winters and mild, moist summers (Johnson 1949). Mean daily temperatures range from −3.3°C in winter to 13.2°C in summer and yearly precipitation averages ~47 cm with 65–75% occurring between the months of April and October (Hoffman and Alexander 1987, Froiland 1990, Shepperd and Battaglia 2002).

On Aug. 24, 2000, the Jasper Fire was ignited near the town of Custer, South Dakota, during a period of record low fuel moisture conditions and extremely unstable atmospheric conditions, leading to strong wind gusts and a maximum rate of spread of 16 ha/min (Lentile et al. 2006). The fire was contained on Sept. 8, 2000, after burning ~34,000 ha of predominantly second-growth ponderosa pine forests in the Black Hills National Forest (US Forest Service 2000). The Jasper Fire was a mixed-severity fire that produced a combination of surface fire, passive crown fire, and active crown fire (US Forest Service 2000).

Experimental Design

After the fire and in collaboration with Black Hills National Forest staff, we identified three 800-ha forest units in which no postfire silvicultural activities (e.g., salvage harvesting) would occur. In June 2001, we randomly established 36 0.3-ha permanent study sites in burned and unburned ponderosa pine stands within and immediately outside the Jasper Fire perimeter. Each forest unit contained three replicates of each fire severity class. Sites were randomly established within fire severity classes, which we assigned on the basis of estimates of crown and forest floor damage from aerial photographs (Table 1). Within the burned stands, nine sites were located in areas in which overstory trees were estimated to have <25% crown damage (treatment = low severity), nine sites were located in stands containing overstory trees that were estimated to have >25% but <100% total crown damage (treatment = moderate severity), and nine sites were located in stands in which all trees experienced ~100% crown consumption (treatment = high severity). The remaining nine sites were located in adjacent unburned pine stands and served as our control sites (treatment = unburned).

Overstory Measurements

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

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

We measured above- and below-canopy photosynthetically active radiation (PAR), in μmoles·m^{-2}·second^{-1}, annually between 2001 and 2005 using a ceptometer (Decagon Devices, Inc., Pullman, WA). Light samples, measured between the hours of 1000 and 1500 Mountain standard time between June and August, were taken in each cardinal direction at 10 points in each overstory plot and averaged for each site. Above-canopy PAR measurements were taken in clear, unobstructed forest openings every 15 minutes and averaged for each site. Percent canopy light transmittance for each site was calculated as (below-canopy PAR/open canopy PAR) × 100. The 2002 PAR data set was incomplete and therefore not included in the analysis.

Forest Floor Measurements

We quantified the effects of wildfire on the forest floor by measuring litter and duff depth and surface woody fuel biomass. Litter and duff depths were measured every 2 m along a 60-m transect that ran 30 m east and 30 m west of each site center. Litter was measured annually from 2001 to 2005 and duff from 2002 to 2005. From these data a yearly site average was calculated. Using bulk densities specific for Black Hills ponderosa pine litter (60.7 kg/m^3) and duff (102.6 kg/m^3) developed by Battaglia (2007), we converted litter and duff depths to estimates of forest floor mass (Mg/ha). Both FWD (Mg/ha) and CWD (Mg/ha) were sampled at each site using the planar intersect method described by Brown et al. (1982). Fine fuels were measured along 10 m of the 60-m transect and coarse fuels were measured along the entire transect.

Table 1. Description of fire severity classes. Percentage of landscape burned in each fire severity class reported by Lentile et al. (2005)

Fire severity class	Percentage of landscape	Description
Unburned	N/A	Sites located in adjacent unburned pine stands; serve as "preburn" reference point and basis for postfire recovery
Low	25	<25% crown scorch with no crown consumption; litter and duff partially consumed; no bare mineral exposed
Moderate	48	>25% crown scorch with partial crown consumption; majority of litter and duff consumed
High	27	~100% of needles consumed; litter and duff completely consumed, resulting in exposure of bare mineral soil

Postfire Tree Regeneration

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

Soil Nitrogen

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

Statistical Analysis

Prefire stand density, BA, average stand diameter, and height to live crown were analyzed as a one-way analysis of variance (ANOVA) to determine whether prefire stand structure varied among fire severities. Postfire measurements and yearly changes in overstory attributes, canopy light transmittance, postfire tree regeneration, litter and duff mass, FWD and CWD, and plant-available nitrogen were analyzed as a repeated-measures ANOVA to determine the effects of fire severity (unburned, low, moderate, and high) and time (1–5 years postfire) on postfire overstory and forest floor development (SAS Institute 2005). Covariance structures for the repeated-measures analyses were modeled as either a first-order autoregressive model or a first-order autoregressive model with heterogeneous variances with site included as a random variable. Separate ANOVAs were performed to test the effect of fire severity each year because the repeated measures analysis indicated significant severity × year interactions for almost all response variables. After significant F test results, pairwise multiple comparisons among treatments were performed using least significant difference (LSD) (Steel et al. 1997). Response variables were $\log_e(n + 1)$ transformed, $\sqrt{n}$ transformed, or $\arcsin\sqrt{n}$ transformed when necessary to approximate normality and homoscedasticity (Steel et al. 1997). The means and SEs we report are from the raw, untransformed data. Analyses were significant at $\alpha = 0.05$.

Results

Prefire Forest Structure and Direct Fire Effects

Before the Jasper Fire, our research sites were well-stocked, second growth, even-aged ponderosa pine stands. Stand density averaged ~670 stems/ha and BA was 24 m^2/ha (Table 2). Stands contained moderately sized trees and had an average stand diameter of ~22 cm. Mean height and height to live crown were ~13 and 5.5 m, respectively. Prefire density, BA, average stand diameter, and height to live crown did not differ among fire severities ($p > 0.17$). Therefore, the subsequent changes in postfire forest structure were attributed to fire-caused damage to the existing prefire vegetation.

The maximum height of crown scorch ranged from ~8 m in low severity sites to ~14 m in high severity sites. These scorch heights translated into total crown damage values of approximately 30, 85, and 100% in low, moderate, and high severity sites, respectively (Figure 1). Basal char was similar between low and moderate severity sites and averaged ~9 ± 4 and 19 ± 6%. Basal char in high severity sites averaged 55 ± 8%, significantly greater than that in both low and moderate severity sites.

Tree Mortality

Initial tree mortality varied in response to fire severity with fire-caused mortality occurring throughout all 5 years of the study. Complete overstory mortality occurred immediately after the fire in areas that burned under high severity.

Table 2. Prefire and 5-year postfire stand structure (live trees ≥5 cm dbh) in unburned, low, moderate, and high severity sites

	Prefire				2005				
Fire severity	Live tree density (trees/ha)	Live BA (m^2/ha)	Average stand diameter (cm)	Height to live crown (m)	Live tree density (trees/ha)	Live BA (m^2/ha)	Average stand diameter (cm)	Height to live crown (m)	CLT (%)
Unburned	727 (109)	24.8 (1.1)	21.8 (1.1)	5.8 (0.6)	714^a (104)	26.3^a (1.0)	22.6^a (1.1)	6.5^a (0.6)	36^a (2)
Low	667 (137)	23.2 (2.5)	22.5 (1.3)	5.0 (0.6)	474^b (43)	21.3^a (2.1)	24.2^a (1.1)	6.7^a (0.7)	51^b (3)
Moderate	521 (59)	23.0 (2.1)	24.3 (0.6)	5.6 (0.5)	190^c (41)	10.8^b (2.0)	27.6^b (1.0)	9.9^b (0.5)	68^c (3)
High	757 (86)	24.1 (1.5)	21.1 (1.0)	5.9 (0.3)	NA	NA	NA	NA	85^d (2)
$P > F$	0.2062	0.8164	0.1777	0.5212	$<$0.0001	$<$0.0001	0.0099	0.0003	$<$0.0001

Analyses were performed on $\log_e$(live tree density + 1), $\sqrt{\text{BA}}$ and $\arcsin\sqrt{}$(canopy light transmittance [CLT]) transformed data. Values represent the untransformed mean (±1 SE). Means followed by the same letter are not significantly different within a column at $\alpha = 0.05$ based on the F protected LSD procedure. NA, not applicable.

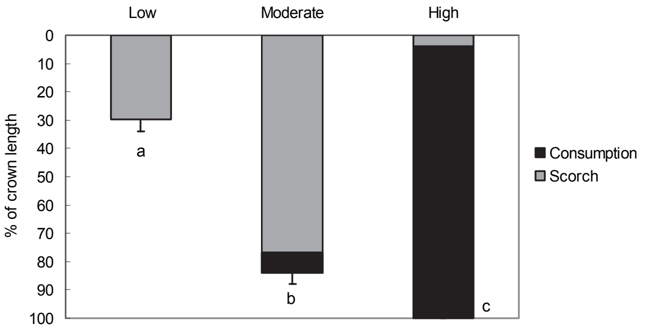

Figure 1. Proportion of crown damage due to scorch and consumption in low, moderate, and high severity sites. Total crown damage is the sum of crown scorch and consumption. Analysis of crown damage data was performed on $\sqrt{}$arcsin-transformed data. Different letters indicate statistical differences in total crown damage among fire severities at $\alpha = 0.05$ based on the F-protected LSD procedure. Values presented are the untransformed mean total crown damage ± 1 SE.

Consequently, we limit comparisons of postfire forest structure through time and among fire severities to unburned sites and those sites that burned under low and moderate fire severity. Small tree density (trees $\geq$5 cm and $<$15 cm dbh) varied among fire severities within individual years (F = 3.0, df = 8, 95.6; $P = 0.0051$) (Figure 2a). At the end of 5 years, moderate fire severity resulted in a 100% reduction in small tree density. In comparison, at the end of 5 years, small tree density in low severity sites had been reduced by 64% from prefire levels.

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

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

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

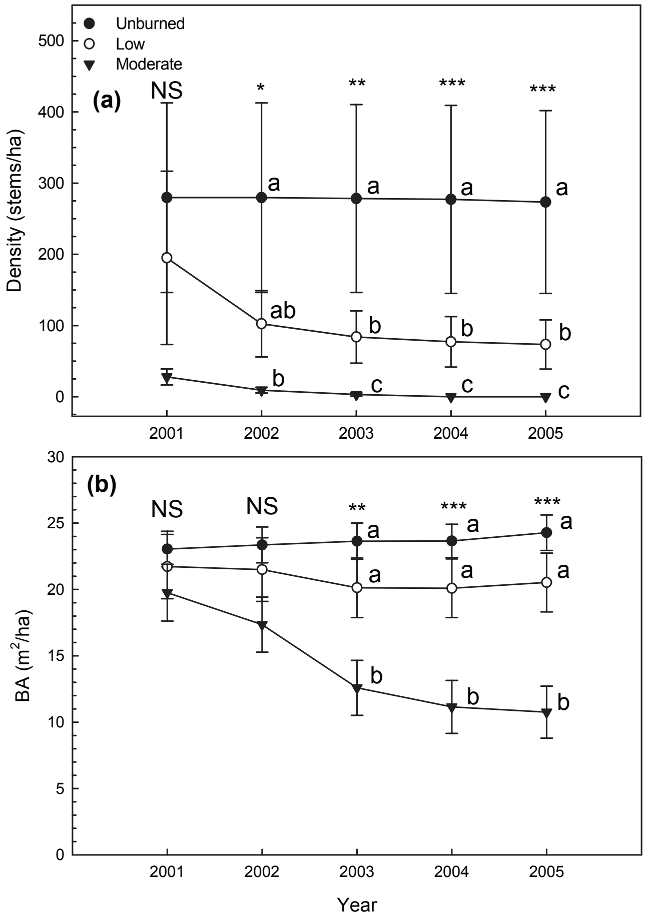

Figure 2. (a) Density (live trees/ha) of trees $\geq$5 cm and $<$15 cm dbh and (b) BA (m^2/ha) of live trees $\geq$15 cm dbh in unburned, low, moderate, and high severity sites. Individual year analyses were performed after significant a severity × year interaction in the repeated-measures analysis of density ($P < 0.05$) and BA ($P < 0.0001$). Analysis of BA data was performed on $\sqrt{}$(BA)-transformed data and analysis of density data was performed on $\log_e$(live tree density + 1)-transformed data. Values presented are the untransformed mean ± 1 SE. Asterisks signify significance within a given year: *$P < 0.05$; **$P < 0.01$; ***$P <$ 0.001; NS, not significant. Means followed by the same letter within a given year are not significantly different at $\alpha = 0.05$ based on the F-protected LSD procedure.

Stand Structure

The accumulated mortality of small and mid-sized trees after low severity fire resulted in a significant reduction in overall stand density from that observed in unburned stands; however, overall BA remained unchanged (Table 2). In moderately burned sites, mortality within all size classes resulted in a significant reduction in overall stand density as well as stand BA. The complete mortality of small diameter trees increased average stand diameter by 5 cm in moderate severity sites whereas enough small diameter trees remained in low severity sites that average stand diameter remained

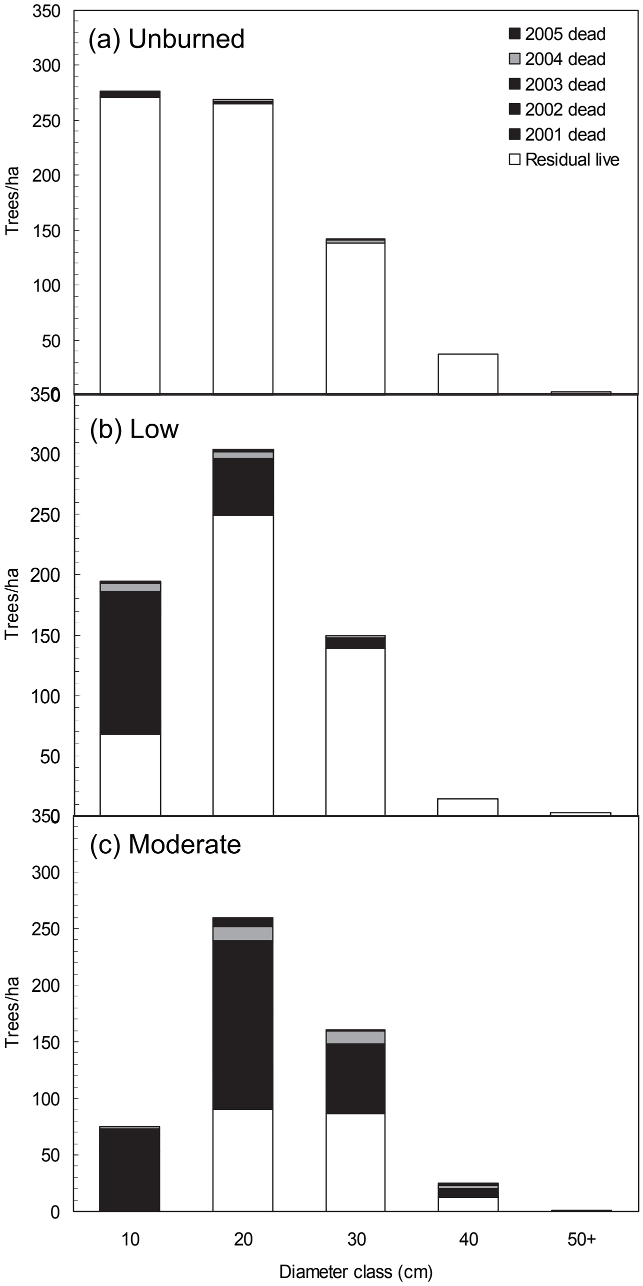

Figure 3. Incremental and accumulated mortality by diameter class in (a) unburned, (b) low, and (c) moderate severity sites from 2001 through 2005.

similar to that of unburned stands. Height to the base of the live crown increased in moderate severity sites by an average ~3.5 m over that in comparable unburned stands, whereas the relative abundance of small and mid-sized trees in low severity sites kept the height to live crown similar to that in unburned stands.

Canopy light transmittance increased with increased fire severity ($F = 70.1$, df = 3, 43.6; $P < 0.0001$). The lowest light levels were observed in unburned sites where only minor levels of overstory mortality were recorded throughout the study period and where an average of only 36% of PAR reached the forest floor (Table 2). As fire-caused mortality occurred in burned stands over the 5 year measurement period, canopy light transmittance increased and resulted in an average of 15, 32, and 49% more PAR in areas of low, moderate, and high severity than in unburned stands.

Forest Floor

Litter mass varied in response to fire severity within individual years ($F = 13.4$, df = 12, 41.4; $P < 0.0001$). Compared with unburned sites, litter was initially reduced by 68% in low severity sites, 88% in moderate severity sites, and 92% in high severity sites (Table 3). Two years postfire, after the abscission of scorched needles, litter mass increased to ~10 Mg/ha in both low and moderate severity sites but remained lower than in unburned sites. At the end of 5 years, litter mass in low severity sites was within 25% of that in unburned stands, and litter mass in moderate severity sites was only 36% less than that in comparable unburned sites. No increase in litter occurred on high severity sites throughout the study.

Fire severity had a significant influence on the recovery of the duff layer; however, the effect of fire severity varied within individual years ($F = 2.2$, df = 9, 51.6; $P < 0.0368$). Compared with an average duff mass of ~29 Mg/ha in unburned sites, duff was reduced by ~89, 95, and 98% in areas of low, moderate, and high severity 2 years postfire (Table 3). Little change in the duff layer occurred 5 years postfire at which time duff had only slightly increased in low and moderate severity sites. Similar to litter, there was no increase of duff mass in high severity sites at any time during the study.

The response of FWD to fire severity varied within individual years ($F = 3.3$, df = 12, 52.9; $P = 0.0014$). One year postfire, FWD in low, moderate, and high severities was reduced by 64, 80, and 92%, respectively compared with that in unburned stands (Table 4). Between 2 and 5 years postfire, FWD steadily increased in both moderate and high severity sites such that at the end of 5 years, FWD had

Table 3. Litter mass and duff mass within each fire severity class 1, 2, 3, 4, and 5 years after the Jasper fire

	Litter mass (Mg/ha)					Duff mass (Mg/ha)			
Fire severity class	2001	2002	2003	2004	2005	2002	2003	2004	2005
Unburned	16.1^{a} (1.5)	14.6^{a} (1.3)	15.9^{a} (1.1)	15.7^{a} (1.2)	16.3^{a} (0.8)	28.2^{a} (2.6)	22.4^{a} (1.3)	21.9^{a} (1.6)	25.2^{a} (1.8)
Low	5.1^{b} (0.5)	9.5^{b} (1.1)	10.5^{b} (1.3)	12.5^{b} (0.7)	12.3^{b} (0.5)	3.2^{b} (1.3)	3.4^{b} (0.8)	4.2^{b} (0.6)	5.5^{b} (0.8)
Moderate	2.0^{c} (0.3)	9.7^{b} (1.3)	11.1^{b} (0.8)	11.5^{b} (0.7)	10.4^{c} (0.9)	1.4^{bc} (0.8)	3.0^{b} (0.5)	3.0^{b} (0.4)	4.1^{b} (0.8)
High	1.3^{d} (0.6)	1.4^{c} (0.3)	2.9^{c} (0.5)	0.7^{c} (0.2)	1.1^{d} (0.3)	0.7^{c} (0.7)	0.4^{c} (0.2)	0.3^{c} (0.2)	0.3^{c} (0.1)
$P > F$	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Individual year analyses were performed after a significant severity × year interaction ($P < 0.05$) in the repeated-measures analysis. Analyses were performed on $\sqrt{}$(litter mass) and $\sqrt{}$(duff mass) transformed data. Values presented represent the untransformed mean (±1 SE). Means followed by the same letter are not significantly different within a given year ($\alpha = 0.05$) based on the F protected LSD procedure.

Table 4. Surface woody fuel loadings for FWD and CWD within each fire severity class 1, 2, 3, 4, and 5 years after the Jasper fire

	FWD (<7.62 cm) surface woody fuel load (Mg/ha)					CWD (>7.62 cm) surface woody fuel load (Mg/ha)				
Fire severity	2001	2002	2003	2004	2005	2001	2002	2003	2004	2005
Unburned	5.9^{a} (1.3)	5.3^{a} (1.3)	6.9^{a} (1.1)	10.1^{a} (1.6)	10.2^{a} (1.6)	14.0^{a} (2.9)	14.6^{a} (3.5)	14.8^{a} (3.3)	15.4 (3.0)	17.2^{a} (3.2)
Low	2.1^{b} (0.4)	2.5^{bc} (0.8)	3.3^{b} (0.6)	3.2^{b} (0.8)	4.1^{b} (0.7)	2.9^{b} (1.0)	4.9^{b} (2.8)	3.5^{b} (1.3)	5.7 (1.6)	6.7^{b} (2.1)
Moderate	1.2^{bc} (0.3)	2.7^{ab} (0.7)	3.1^{b} (0.6)	5.0^{b} (1.4)	12.5^{a} (3.3)	2.2^{b} (1.3)	3.1^{b} (1.5)	3.2^{b} (1.3)	9.3 (3.9)	19.8^{ac} (5.3)
High	0.5^{c} (0.2)	0.8^{c} (0.4)	1.7^{b} (0.6)	6.5^{ab} (1.6)	14.1^{a} (2.2)	3.4^{b} (1.4)	6.0^{b} (3.2)	6.9^{b} (3.6)	14.1 (3.2)	30.0^{c} (3.1)
$P > F$	<0.0001	0.0052	0.0006	0.0057	0.0160	<0.0001	0.0164	0.0075	0.0605	0.0011

Individual year analyses were performed after a significant severity × year interaction ($P < 0.05$) in the repeated measures analysis. Analyses were performed on the $\sqrt{}$(FWD) and $\sqrt{}$(CWD) transformed data. Values represent the untransformed mean (±1 SE). Means followed by the same letter are not significantly different within a given year ($\alpha = 0.05$) based on the F protected LSD procedure.

recovered to unburned levels. The reductions in FWD in low severity sites remained, however, with FWD being 60% lower than that in comparable unburned stands 5 years postfire.

The amount of CWD in burned sites was influenced by fire severity whereas recovery within fire severity classes varied within individual years ($F = 5.6$, df = 12, 67.3; $P <$ 0.0001). Consumption of CWD during the fire caused a significant reduction in CWD in burned sites, regardless of fire severity, compared with CWD in the nearby unburned stands (Table 4). Compared with unburned sites, initial reductions in CWD in low, moderate, and high severity sites were 83, 86, and 81%, respectively. Five years postfire, CWD in low severity sites remained 61% lower than that in unburned sites; however, CWD in moderate severity sites increased 800% over 2001 levels and was equal to that in unburned sites. The largest 5-year increase in CWD occurred in high severity sites in which CWD loads increased from 3 Mg/ha 1 year postfire to 30 Mg/ha 5 years postfire; almost twice the level observed in unburned stands.

Postfire Tree Regeneration

Postfire tree regeneration was variable throughout the 5-year study; however, it was significantly influenced by the interaction between fire severity and year ($F = 9.9$, df = 9, 40.5; $P < 0.0001$). Little to no relationship was observed between fire severity and the amount and success of postfire tree regeneration among unburned, low, and moderate severity sites. Generally, unburned sites possessed equal or slightly greater amounts of tree regeneration than low and moderately burned sites (Figure 4). As time progressed, postfire tree regeneration in high severity sites, however, was consistently lower than that observed in unburned, low, and moderate severity sites.

Soil Nitrogen

The influence of fire severity on available nitrogen varied yearly ($F = 7.1$, df = 9, 55.1; $P < 0.0001$). Fire severity had a significant effect on available nitrogen 1 year postfire with burned sites having greater nitrogen availability than unburned sites (Figure 5). Between 1 and 5 years postfire, there was a progressive and steady decline of plant-available nitrogen within burned sites. At the end of 5 years, available nitrogen had been reduced to that of unburned conditions in low and moderate severity sites; however, available nitrogen continued to be elevated above unburned levels in areas that experienced high fire severity.

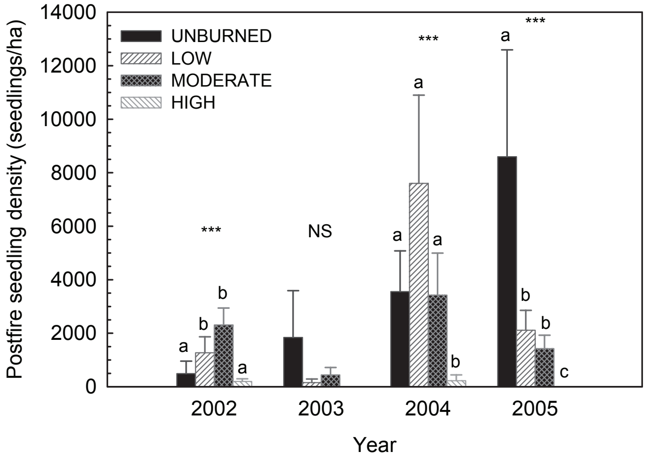

Figure 4. Cumulative postfire seedling density (seedlings/ha) within each fire severity class. Individual year analyses were performed after a significant severity × year interaction ($P < 0.0001$) in the repeated-measures analysis. Regeneration was not aged in 2001 and therefore not included. Analysis of seedling density data was performed on $\log_e$(seedling density + 1)-transformed data. Values presented in the figure represent the untransformed mean ± 1 SE. Asterisks signify significance within a given year: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS, not significant. Means followed by the same letter within a given year are not significantly different at $\alpha = 0.05$ based on the F-protected LSD procedure.

Discussion

We asked specifically how differences in fire severity affected the processes and rate of ecological recovery with respect to key components of vegetation structure, tree regeneration, and forest floor. The Jasper Fire burned as a single event but created a mosaic of fire severity and initial fire effects across a 34,000-ha landscape (US Forest Service 2000). The majority of patches created by the Jasper Fire burned under low and moderate severity. The average size of low severity patches was small, ~10 ha; however, 38% of patches were between 100 and 1,000 ha and 30% were >1,000 ha (Lentile et al. 2005). The average patch size of moderate severity was 24 ha with 38% of the patches ranging in size from 100 to 1,000 ha and 40% of the patches >1,000 ha (Lentile et al. 2005). The smallest average patch size was observed in areas affected by high fire severity. Here, patch size averaged only 7.5 ha with 60% of patches between 1 and 15 ha and 15% <1 ha (Lentile et al. 2005).

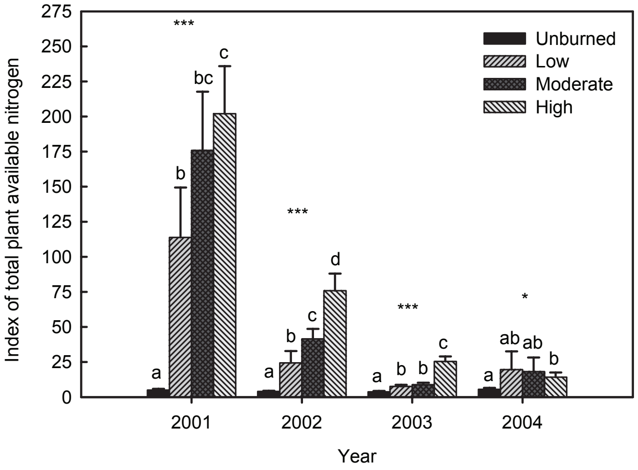

Figure 5. Index of total plant-available nitrogen within each fire severity class. Individual year analyses were performed after a significant severity × year interaction ($P < 0.0001$) in the repeated-measures analysis. Analysis of total nitrogen data was performed on $\log_e$(total nitrogen + 1)-transformed data. Values presented in the figure represent the untransformed mean ± 1 SE. Asterisks signify significance within a given year: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; NS, not significant. Means followed by the same letter within a given are not significantly different at $\alpha = 0.05$ based on the F-protected LSD procedure.

Unlike low and moderate severity for which patch sizes exceeded 1,000 ha, the largest patch of high fire severity was 900 ha (Lentile et al. 2005). The future forested landscape will be a composite of the mosaic of fire severities and the patterns of forest development that ensue as a consequence of changes to overstory forest structure and to the forest floor. Substantial differences in postfire structure and subsequent ecological recovery within this ponderosa pine forest resulted from differences in fire severity.

Little change in forest structure occurred as a result of low fire severity (Figure 2). The structure produced as a result of low fire severity was similar to that achieved via a mechanical low-thinning. Similar to unburned stands, stands affected by low fire severity continued to be a single-canopied forest with little opportunity for further overstory recruitment. These sites maintained full-site occupancy (Long and Smith 1984). Consequently, these sites will continue to contribute to the timber base and future timber production in the Black Hills. In terms of fuels reduction efforts, the low severity surface fires, which occurred over 25% of the burned landscape (Lentile et al. 2005), accomplished what most fuels reductions efforts are designed to do: reduce unnaturally high surface fuel loadings and the potential for severe fire behavior (Agee and Skinner 2005). Although the average height to the base of the live crown was not increased in low severity sites relative to unburned stands, a reduction in both FWD and CWD and duff mass may reduce flame lengths and fire severity in future wildfire or prescribed fire events, which decreases the potential for torching and simplifies fire control efforts (Agee and Skinner 2005). The lack of mortality in the larger canopy trees, however, maintains a canopy fuels structure (e.g., high canopy bulk density) that may continue to be susceptible to crown fire under severe weather conditions (Keyes and O'Hara 2002, Agee and Skinner 2005).

Areas burned under moderate severity experienced a significant and substantial reduction in overstory canopy density with complete mortality of small trees and a ~50% reduction in large tree density (Figure 2). Mortality throughout the size classes left these stands well below the threshold for full-site occupancy (Long and Smith 1984), thereby reducing the ability of these stands to supply timber resources well into the future. The removal of the smaller diameter ladder fuels decreased vertical and horizontal continuity of the canopy fuel stratum and, coupled with the dominance of the stand by larger, more fire-resistant trees (Keyser et al. 2006), substantially reduced the risk of active crown fire in future fire events (Agee and Skinner 2005). The open stand structure created by moderate fire severity, with few large surviving trees, is similar to ecological restoration treatments applied in Southwestern ponderosa pine forests that are designed to protect large diameter trees from crown fire, reduce tree competition, and restore pre-Euro-American forest structure (Fulé et al. 2002). The survival and retention of large, seed-bearing trees within moderate severity sites ensures a seed source for future regeneration. With low overstory density and increased light transmittance, overstory recruitment of postfire seedlings is likely, which will ultimately result in the development of a multistoried forest structure. Over time, this structure, which is currently uncommon in the Black Hills (Shepperd and Battaglia 2002), will increase structural diversity throughout the burned landscape.

Substantial fuel accumulation occurred throughout the 5 years after the Jasper Fire in both moderate and high severity sites. Although fire hazard in these stands is not of particular importance in the short-term (Brown et al. 2003), continued snag fall and fuel accumulation (e.g., Passovoy and Fulé 2006) within these sites may result in an increase in fire intensity and severity (DeBano et al. 1998, Brown et al. 2003, Skinner 2005) in a reburn event. These fire hazards will only escalate as fallen snags decay and transition from solid to rotten biomass (DeBano et al. 1998, Passovoy and Fulé 2006). Five years postfire, the opportunities for fuels reduction treatments within these sites were limited. The creation of heavy slash fuels due to snag-fall creates a situation in which fuels reduction via prescribed fire is a high-risk option for forest managers. In addition, fire effects and fire behavior associated with heavy slash fuels would probably have negative effects on forest soils and vegetation because of the increased fire severity associated with high fuel loads (DeBano et al. 1998). Alternatively, models (e.g., the Fire and Fuels Extension to the Forest Vegetation Simulator [FFE-FVS]) suggest that salvage operations during the immediate months postfire have the potential to limit CWD accumulation after high severity wildfire (Brown et al. 2003, McIver and Ottmar 2007), potentially reducing fire severity in future reburn events (US Forest Service 2002).

Disturbance to overstory vegetation and the forest floor interact to influence the development of stands affected by wildfire. In combination with increased light, reduced litter and duff depth, increased available nitrogen, and the presence of residual seed trees, we expected to see significantly greater rates of seedling germination and establishment (e.g., Bailey and Covington 2002) within low and moderate severity sites as good seed production every 2–5 years (Boldt and Van Deusen 1974) and a favorable growing season climate promote abundant regeneration in the Black Hills. Instead, regeneration was sporadic, which was probably due to prolonged drought conditions after the fire (Figure 4). Brown and Wu (2005) found that prolific regeneration and recruitment of ponderosa pine before Euro-American settlement in southwestern Colorado occurred only when disturbances opened portions of the canopy concurrent with or followed by periods of ample moisture. In the Black Hills, germination and establishment of ponderosa pine seedlings has not been shown to be negatively affected by competing understory vegetation owing to plentiful precipitation during the growing season (Wagar and Meyers 1958). Therefore, even with the rapid reestablishment of competing understory vegetation (Keyser 2007), given adequate moisture in the future, significant regeneration in low and moderate severity sites similar in amount to or exceeding that in unburned stands can be expected (Battaglia 2007).

A different scenario exists in areas that experienced high fire severity. Regeneration and overstory development after stand-replacing wildfire has been shown to vary considerably in ponderosa pine forests. Closed-canopied forest, shrubland, and grass/forb-dominated meadows are cover types produced after stand-replacing wildfire in the Southwest (Savage and Mast 2005). The return of these stands to a late-successional forest will depend on patch size and proximity to seed source. Dispersal of ponderosa pine seed is limited to 1 to 1.5 times tree height (Shepperd and Battaglia 2002). Therefore, as patches of high fire severity increase in size, the proximity to an off-site seed source decreases, limiting regeneration of heavy-seeded ponderosa pine to forest edges (Savage and Mast 2005, Bonnet et al. 2005). The need to artificially stock these stands will have to be dealt with on a stand-by-stand basis and will ultimately depend on management goals and objectives. If postfire objectives include a rapid return of large, high severity patches to the timber base, artificial planting will be required, especially in the 32% of high severity patches between 100 and 1,000 ha (Lentile et al. 2005). However, if returning stands to timber production is not the primary management goal, but maintaining newly created wildlife habitat and increasing biodiversity are considered important in postfire management plans, no direct action would be necessary. Before the Jasper Fire, only 2% of the Black Hills landscape was classified as nonstocked (DeBlaner 2002), substantially less than the acreage noted by Graves (1899) before Euro-American settlement. Limiting postfire rehabilitation (e.g., artificial planting) efforts in these stands would increase structural heterogeneity and potentially maintain vegetation and cover types that are rare within this heavily managed, forested landscape.

Before the Jasper Fire, the landscape was a homogeneous second-growth, closed-canopied ponderosa pine forest. Five years postfire, it was a heterogeneous landscape with a complex mosaic of different stand structures and cover types that developed as a result of different fire severities. Approximately 25% of the landscape experienced low fire severity (Lentile et al. 2005), which did not significantly alter overstory structure but did significantly modify the structure and composition of the forest floor. In contrast, the 48% of stands that burned under moderate fire severity (Lentile et al. 2005) are now open, low-density stands consisting of only large diameter ponderosa pine that, over time, will probably develop into an multistoried forest structure. Although the overstory structure of these stands is substantially different from that of the surrounding forest, the woody fuel bed is similar to that of the unburned forest. Unless artificially stocked, portions of the 27% of the area that experienced high fire severity (Lentile et al. 2005) that are outside the range of a potential seed source will probably remain open herbaceous/shrublands (Savage and Mast 2005) and possess woody fuel loads above that of the surrounding forest for decades. The amount of CWD on the landscape is a product of decomposition and accumulation rates (Sturtevant et al. 1997). Therefore, if these high severity forest stands do not regenerate, the long-term maintenance of the surface woody fuel layer will be limited by future inputs (Spies et al. 1988).

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

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