Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA

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Abstract: We compared patch structure, fire-scar formation, and seedling regeneration in patches of low, moderate, and high burn severity following the large (~34 000 ha) Jasper fire of 2000 that occurred in ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) forests of the Black Hills of South Dakota, USA. This fire created a patchy mosaic of effects, where 25% of the landscape burned as low, 48% as moderate, and 27% as high severity. 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. Tree mortality was approximately 21%, 52%, and 100% in areas of low, moderate, and high burn severity, respectively. Dead cambium was detected on approximately 24% and 44% of surviving trees in low and moderate burn severity patches, respectively. Three years postfire, regeneration densities were ~612 and 450 seed-lings·ha⁻¹ in low and moderate burn severity patches, respectively, and no regeneration was observed in the interior of high burn severity patches. Fire-scars will be found on 73% of the area burned in this fire, and large patches of multicohort forest will be created. Mixed-severity fire may have been common historically in the Black Hills, and in conjunction with frequent surface fire, played an important role in shaping a spatially heterogeneous, multicohort ponderosa pine forest.

Résumé : Les auteurs ont comparé la structure de morcellement, la formation de cicatrices de feu et la régénération d'espèces arborescentes dans des parcelles brûlées à faible, moyenne et forte intensités à la suite du grand feu (~34 000 ha) de Jasper survenu en 2000 dans des forêts de pin ponderosa (*Pinus ponderosa* Dougl. ex P. & C. Laws.) de la région des Black Hills dans le Dakota du Sud, aux États-Unis. Ce feu a créé une mosaïque morcelée d'effets dans laquelle 25% de la superficie a été brûlée à faible intensité, 48 % à intensité modérée et 27 % à forte intensité. La présence de cambium mort sur une portion importante de la circonférence d'un arbre ayant toujours du cambium vivant et une cime vigoureuse a été utilisée comme indice de la formation imminente d'une cicatrice de feu. Le taux de mortalité des arbres atteignait respectivement environ 21, 52 et 100 % dans les aires brûlées à intensités faible, modérée et forte. Du cambium mort a été détecté sur respectivement environ 24 et 44 % des arbres survivants dans les aires brûlées à intensités faible et modérée. Trois ans après le feu, la densité de régénération était respectivement de 612 et 450 semis-ha⁻¹ dans les aires brûlées à forte intensité. Des cicatrices de feu seront présentes sur 73 % de la superficie brûlée par ce feu et de grandes superficies de forêt à étages multiples seront créées. Des feux d'intensité variable ont pu être courants dans le développement d'une forêt à plusieurs étages et spatialement hétérogène de pin ponderosa.

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Introduction

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

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¹Corresponding author (e-mail: lentile@uidaho.edu). ²Present address: Department of Forest Resources, University of Idaho, Moscow, ID 83844, USA. these conditions is increasingly a goal of management (Morrison and Swanson 1990; Covington et al. 1997; Arno et al. 2000). The role of fire in western forests has been inferred largely from examination of basal fire-scars (Weaver 1951; Arno and Sneck 1977; Baisan and Swetnam 1990; Brown et al. 1999) or stand structure and establishment patterns (Cooper 1960; Lorimer 1985; Fulé et al. 1997; Kaufmann et al. 2000). However, the relation between evidence of fire occurrence and burn severity is poorly understood (Mutch and Swetnam 1995), and opportunities to validate sampling and interpretation of fire-history evidence have been limited (Baker and Ehle 2001; Fulé et al. 2003). We examined fire effects that are used as evidence of fire behavior and severity following a contemporary large mixed-severity fire in ponderosa pine (Pinus ponderosa Dougl. ex P. & C. Laws.) forests of the South Dakota Black Hills.

Mixed-severity fire regimes are complex and perhaps the most poorly understood of all fire regimes in the western United States (Agee 1996; Chappell and Agee 1996; Fulé et al. 2003). Mixed-severity fire regimes have elements of surface, torching, and active crown fire behavior and therefore exhibit heterogeneous fire effects that leave some dead and some surviving vegetation in patches of various sizes (Agee 1998; Kaufmann et al. 2000). Mixed-severity regimes may include individual fires that create variable fire effects those dominated by stand-replacing or lethal components, as well as fires dominated by surface fire behavior (Arno et al. 2000; Agee 2005). Variation in intensity and severity due to weather, topography, and vegetation type and structure occurs even within large fires (Eberhard and Woodward 1987; Turner et al. 1994), and heterogeneous or "mixed" effects occur at some scale in all fires. This variation complicates the ability to retrospectively attribute causality and make inferences about the nature of these fire regimes.

Fire-history methods are difficult to apply in mixed-severity fire regimes because most techniques have been developed to study historical conditions in either low- or high-severity regimes (Agee 2005; Hessburg et al. 2005). The frequency, timing, and, in some cases, extent of surface fire have been inferred from the presence of fire scars in a population of surviving trees and widely applied to characterize low-severity fire regimes (Baisan and Swetnam 1990; Brown and Sieg 1996; Fulé et al. 1997). Although the presence of fire scars is generally considered evidence of surface fire, the relationship between severity and fire-scar formation in wildfires has not been well quantified. Physical descriptions of fire-caused tree damage and physiological explanations for cambial death on trees of various sizes have been developed under simulated or controlled conditions (Fahnestock and Hare 1964; Vines 1968; Gill 1974; Gutsell and Johnson 1996). In Sequoia and Kings Canyon National Park, California, Mutch and Swetnam (1995) quantified severity following prescribed fire by ring-width growth and concluded that growth response patterns could be used to infer fire severity of older fires. However, interpretation of repeated fire scars on a tree or in a population may not provide conclusive evidence of the type of fire behavior that created the series of fire scars, particularly across entire landscapes (Mutch and Swetnam 1995; Baker and Ehle 2001).

In high-severity fire regimes, techniques based on ageclass analysis including natural fire rotation (Heinselman 1973; Morrison and Swanson 1990; Agee and Krusemark 2001) or fire cycle (Johnson and Van Wagner 1985; Johnson and Larson 1991) are used to describe the extent and frequency of fires (Johnson and Gutsell 1994; Morgan et al. 2001). Landscape patch structure, typically assessed with aerial photography or satellite imagery, has been used to reconstruct fire extent and severity, particularly where stand-replacing fires leave distinct boundaries. Here, the size and spatial distribution of burned and unburned areas may have profound and persistent effects on the reestablishment of plant species on burned sites and the distribution of age-classes on the landscape (Turner et al. 1994; Lertzman et al. 1998; Brown et al. 1999; Kaufmann et al. 2000). However, in landscapes with less distinct spatial gradients, historical fire size and the proportions of severity within a fire are particularly difficult to reconstruct (Agee 1998, 2005).

Both fire-scar and age-class data are necessary to accurately describe the complexity found in mixed-severity fire regimes (Morgan et al. 2001; Agee 2005; Hessburg et al. 2005). In the Blue Mountains of Oregon and Washington,

Heyerdahl et al. (2001) examined fire scars as evidence of low severity and cohort establishment dates as evidence of high and moderate severity to infer the controls of spatial variation in historical fire regimes. Highly variable regimes in terms of fire frequency, severity, and patch size have been documented in the Pacific Northwest Cascade Range (Agee et al. 1990; Morrison and Swanson 1990; Chappell and Agee 1996), the Klamath Mountains of California and Oregon (Taylor and Skinner 1998; Odion et al. 2004), and the Colorado Front Range (Kaufmann et al. 2000, 2003). In a modern calibration for the interpretation of fire-scar results, Fulé et al. (2003) reconstructed fire regime characteristics from fire-scar analysis, remote sensing, tree age, and forest structure measurements and found strong correspondence between fire-scar data and fire-record data for all but very small fires in a mixed-severity fire regime in high-elevation forests of Grand Canyon, Arizona.

There is no characteristic signature or suite of evidences of fire occurrence such as patterns of burn severity, fire-scar formation, and tree age structure uniquely associated with mixed-severity fire regimes (Agee 2005). In mixed-severity regimes, stand-replacing fire can erase surviving trees with multiple fire scars or scars may heal over and scar again following subsequent nonlethal fires. Multiple age-classes of fire-induced tree regeneration are likely to be present in mixedseverity fire regimes. Yet future surface fires or prolonged drought may kill most of the surviving trees or seedlings that are recruited following fire. Patches in mixed-severity regimes are generally intermediate in size, but have more edge than either low- or high-severity regimes; however, this edge may be easily distinguishable through time or fade rapidly following fire (Agee 1998, 2005).

In this paper, our goals were to (1) determine the relation between fire-effects evidence and burn severity; (2) determine the fire-history evidence left by this fire; and (3) place this evidence in the context of discussions about historical fire regimes in the Black Hills (e.g., Brown and Sieg 1996, 1999; Shinneman and Baker 1997; Shepperd and Battaglia 2002; Brown 2003). Specifically, we compared three types of evidence of fire occurrence and severity (i.e., fire-scar formation, patch structure, and tree seedling regeneration) in low, moderate, and high burn severity. We examined surviving trees to determine whether it is possible to detect incipient fire-scar formation. We estimated density of fire-scarred trees in areas of different burn severity and related likelihood of new scar formation to tree size, bark thickness, and preexisting scar presence. We analyzed the spatial distribution of patches of different burn severity. We measured tree survivorship and regeneration in areas of low, moderate, and high burn severity 2 and 3 years postfire to assess developing age structure. Finally, the potential role of surface and mixedseverity fires as components of the presettlement fire regime based on evidence left by the Jasper fire is discussed.

Methods

Study area

The Black Hills is an isolated and forested mountain range rising over 1000 m above the Great Plains of western South Dakota and northeastern Wyoming (Boldt and Van Deusen 1974; Shepperd and Battaglia 2002). As the easternmost ex-

Burn		
severity	Fire type	Fire effects
Low	Surface	<25% canopy scorch; low tree mortality; light ground char; most duff and litter retained
Moderate	Mixed surface fire and torching	>25% canopy scorch; mixed tree mortality and survival; moderate ground char; vegetation and duff retained in patches
High	Stand replacing	Aboveground vegetation, litter, duff, and needles in canopy mostly blackened; 100% tree mortality; litter and duff not retained; heavy ground char with bare mineral soil exposed

Table 1. Description of fire effects within classes of burn severity.

tension of the Rocky Mountains, the Black Hills was formed by regional uplift approximately 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 tremuloides* Michx.) clones and meadowland inclusions are found in the study area. Regeneration of pine through the 20th century has been abundant and relatively constant because of favorable moisture conditions throughout the spring and summer (Shepperd and Battaglia 2002).

In 9 days in the 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, South Dakota. The Jasper fire was ~25% larger than any other recorded fire in Black Hills history (USDA Forest Service 2001) and burned under conditions of very low fuel moisture and high winds (USDA Forest Service 2000; Benson and Murphy 2003). This fire burned in the interior forests of the southern Black Hills, originating near the present-day Jewel Cave National Monument and collection sites for Brown and Sieg's (1996) dendrochronological fire-history research. It burned primarily to the north into the drainages of Upper Hell Canyon and Gillette Canyon (USDA Forest Service 2000), previously described by Graves (1899) as cited by Shinneman and Baker (1997). Many early explorers described effects, extent, and residual patterns of large historical wildfires in the Black Hills (Ludlow 1875; Newton and Jenny 1880; Graves 1899; Gartner and Thompson 1973; Raventon 1994; Dodge 1996). In the 1890s two large fires burned ~31 000 ha in the northern Black Hills, and in the 1930s the Rochford and McVey Fires burned ~17 000 ha on the Limestone Plateau (USDA Forest Service 1948). Although several large fires have been documented in the post-European settlement era, fire suppression has effectively eliminated surface fire since the turn of the century. Currently, there are relatively few places on the Black Hills landscape that resemble historical forest conditions following over a century of grazing, repeated harvest, and effective fire suppression.

Field- and remotely sensed estimates of burn severity

Many contemporary fire studies interpret the physical and ecological changes caused by fire as indicators of severity. Fire intensity and burn severity are often used interchangeably (Parsons 2003; Jain et al. 2004) and are related (DeBano et al. 1998), but describe the behavior and effects of individual fires, respectively (Morgan et al. 2001). Fire intensity is a physical measure of the energy released by a flaming front and is closely correlated with flame length (Byram 1959; Albini 1976). Burn severity has been described by the degree of tree mortality (Chappell and Agee 1996; Morgan et al. 1996), soil heating (Lea and Morgan 1993), organic biomass consumption (Lenihan et al. 1998), change in soil physical properties (Wells et al. 1979), a combination of these fire effects (Turner et al. 1994; Parsons 2003; Key and Benson 2005), or broadly defined as the degree of ecosystem change induced by fire (Ryan and Noste 1985; DeBano et al. 1998; Robichaud et al. 2000).

Fire significantly affects the reflective properties of the land surface because of changes in canopy cover, biomass removal, soil exposure, and soil heating. Stratification of remotely sensed Landsat data combined with visually based field verification has been used to define classes of burn severity (Milne 1986; Jakubauskas et al. 1990; Turner et al. 1994). Furthermore, studies confirm that 1-year postfire images provide satisfactory identification of burn severity (White et al. 1996; Cocke et al. 2005).

Burn severity map

Gould (2003) produced a burn severity map from 30 m spatial resolution Landsat 7 imagery (acquired 24 September 2001). We chose to analyze this image, as it was taken 1 year postfire and was free of cloud and smoke interference. Tree mortality was more evident, and needle loss permitted a clearer satellite "view" of ground conditions. Gould (2003) used the ISODATA (Ball and Hall 1965) algorithm to identify 10 classes of spectral reflectance. Three randomly selected plots were located within each of the 10 ISODATA classes. Gould (2003) assessed fire effects on forest canopy at each plot center and ground conditions in nine subplots (72 points per plot). Groups of pixels or plots exhibiting similar characteristics of fire effects on overstory and understory vegetation and soil were grouped into classes following Ryan and Noste's (1985) severity classification. Burn severity classes ranged from low (surface fire) to moderate (mixed surface fire and torching) to high (stand-replacing fire) (Table 1). Low severity had low tree mortality, predominantly green tree canopies (<25% canopy scorch), and >70% ground cover. Moderate severity had mixed tree mortality and survival, extensively scorched tree canopies (>25% scorch), and 30%-70% ground cover. High severity was characterized by complete tree mortality (100% blackened canopies) and less than 30% ground cover, although typically 10% or less (Gould 2003).

Two independent data sets were used by Gould (2003) to validate the accuracy of the final burn severity map. The first consisted of field observations collected in September 2000 that were then used to calibrate a second and separate product referred to as an initial assessment of fire intensity. Field

Crown vigor	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 2. Classes of crown vigor used to rate the likelihood of tree survival 2 years postfire.

technicians focused primarily on tree canopy scorch as an indicator of the immediate postfire condition of vegetation. Observations and photographs made at each site were compared with the burn severity classifications to determine accuracy. Gould's burn severity map correctly categorized 63% of the low severity areas, 68% of the moderate, and 69% of the high. The second data set was collected during the summer of 2002 and incorporated the same methods used to develop the severity classification. Ten plots were randomly located in each severity class with no prior knowledge of the classification. Sites were reselected if they coincided with areas influenced by postfire salvage logging. This 2-year postfire assessment indicated that Gould's burn severity map correctly classified burn severity for 70%–82% of the sites.

Analysis of burn severity map

We used the Patch Analyst[©] extension in ArcView GIS[®] (ESRI 1998) to examine spatial patterns of burn severity at the landscape level. We used Patch Analyst to create, query, map, and analyze cell-based raster data corresponding to classes created from spectral reflectance values. We created patches by dissolving boundaries between adjacent polygons of the same burn severity class. Class and landscape metrics include number of patches, mean patch size, patch size standard error, median patch size, mean core area, and core area standard error (Elkie et al. 1999). Within high-severity patches, we identified edge areas as within 30 m of a patch containing live trees and core areas as greater than 30 m from a live tree edge and, therefore, potentially vulnerable to cover type conversion because of seed dispersal limitations. We used 30 m as an estimate of maximum effective seed dispersal distance, since ponderosa pine seeds disperse within ~1-1.5 times parent tree height (Boldt and Van Deusen 1974; Shepperd and Battaglia 2002).

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

Plot sampling

We used color infrared aerial photography and Gould's (2003) map of burn severity to identify sampling areas. Study areas contained a mosaic of low, moderate, and high burn severity and were not impacted by postfire management activities. All study areas were located between latitudes 43°41'35"N and 43°55'48"N, longitudes 103°46'01"W–104°00'47"W, and elevations ~1500–2100 m. All plots were permanently located with a Garmin[®] GPS unit.

In 2002, we identified 10 potential study sites from all available burned areas within the ponderosa pine cover type that contained a mosaic of burn severities and had not been harvested postfire. We randomly selected one site for a pilot study. During this preliminary study, we compared the efficacy of tools and identified characteristics that facilitated the differentiation of live and dead cambium. We sampled cambium on 150 trees at 30 cm above the soil surface with an increment hammer, a portable drill with a 3.2 cm steel holesaw 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. We defined the presence of dead phloem on 10% or more of the circumference of a fire survivor as 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. Removal of the sample from the increment hammer was time consuming, and repeated strikes to the tree were often required to obtain one sample for examination. The drill also vielded a reliable sample, but drawbacks included the mass 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 (~10 cm² per strike) 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 was possible to differentiate between live and dead phloem and that both can be found on the same live tree.

We randomly selected five ~600 ha study sites from the remaining nine potential study sites. We measured prefire tree density, fire-caused mortality, incipient fire-scar formation, and tree regeneration densities. Twenty variable-radius (2.2 metric basal area factor) plots were randomly located per severity class within each of the five study sites for a total of 100 plots per burn severity class (N = 15). We located plots in areas of high severity at a minimum distance of 30 m from any surviving trees. Two years postfire, we assessed tree status (live, dead because of fire-kill, prefire dead) and crown vigor (Table 2) on all trees within each plot. We measured diameter and bark thickness at breast 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 phoem was de-

				% of area by patch size (ha)			
Burn severity	% of landscape	No. of patches	Mean patch size (ha)	0-10	10-100	100-1000	>1000
Low	25	824	10.4 (2.7)	15	17	38	30
Moderate	48	647	24.1 (7.1)	8	14	38	40
High	27	1201	7.5 (1.0)	30	38	32	0

Table 3. Distribution, number, and size (with SE in parentheses) of patches in burn severity classes.

Table 4. Comparison of prefire and 2 years postfire stand structure for areas of low, moderate, and high burn severity on five study sites; values are means with SE in parentheses.

	Avg. live stand diameter (cm)		Density (live trees ha ⁻¹)		Live basal area (m ² ·ha ⁻¹)	
Burn severity	Prefire	Postfire	Prefire	Postfire	Prefire	Postfire
Low	27.9 (2.4)	28.4 (1.2)	542.5 (152.0)	499.6 (76.5)	28.6 (4.2)	27.1 (2.6)
Moderate	25.6 (2.1)	28.5 (2.0)	606.3 (162.2)	390.1 (70.2)	27.5 (3.8)	21.0 (1.7)
High	20.7 (0.6)	_	822.8 (287.3)	_	26.4 (1.2)	_
P value	0.0013	0.9281	0.2008	0.0102	0.3792	< 0.0001

Table 5. Comparison of fire-scar formation in trees likely to survive in low- and moderate-severity burns in the five study sites; values are means with SE in parentheses.

Burn severity	Fire-scar formation (%)	Density (trees · ha ⁻¹)
Low	23.6 (1.8)	122.7 (52.8)
Moderate	43.7 (3.7)	162.8 (68.6)

tected 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 preexisting scars or cambial wounds separately. This methodology allowed us to estimate the density of fire scars per hectare as a percentage of the survivors per burn severity.

At each tree plot location, we measured density of ponderosa pine seedlings (trees <1.4 m in height). We recorded seedling status (live or dead) and age in three 3.14 m² randomly located plots for a total of 180 plots in each of five study sites (N = 15). Three years postfire, we returned to each tree plot location to determine tree survival and to randomly sample cumulative ponderosa pine seedling density.

We performed summary and statistical analyses of plot data in SAS version 8.2 (SAS Institute Inc. 2001). We summarized plot data for each class of burn severity at the five study sites. We compared values using analysis of variance (PROC GLM, SAS Institute Inc. 2001). Probabilities were computed to determine whether means were significantly different from each other. We compared the difference between observed and expected fire-scar frequencies in low and moderately burned areas with a χ^2 test (PROC FREQ, SAS Institute Inc. 2001). Variables were tested for significance at the 95% confidence level (P < 0.05).

Results

The Jasper fire was large and the burn mosaic complex. Spatial analysis of Gould's (2003) burn severity map indicated a highly patchy mosaic, where 25%, 48%, and 27% of the landscape was burned by low-, moderate-, and high-

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

Before the fire, the ponderosa pine stands on our five study sites were dense. There were 543, 606, and 823 live trees ha^{-1} , respectively, in areas of low, moderate, and high severity. Prefire average stand diameter was 27.9, 25.6, and 20.7 cm, respectively, in areas of low, moderate, and high severity. Prefire live basal areas were 28.6, 27.5, and 26.4 m² ha^{-1} , respectively, in areas of low, moderate, and high severity. Prefire stand density and basal area were not statistically different in areas of different burn severity (P < 0.05) (Table 4).

We examined ~3800 trees 2 years following fire and found 5.5%, 23.8%, and 100% mortality, respectively, in areas of low, moderate, and high severity (Fig. 1). Significantly more trees died, and they were significantly smaller in moderately burned areas than in low severity burned areas. Average DBH for fire-killed trees was 25.2, 20.9, and 20.7 cm, respectively, in areas of low, moderate, and high severity. After the fire, we found 500 and 390 live trees ha⁻¹, respectively, in areas of low and moderate severity. Postfire live basal areas were 27.1 and 21.0 m²·ha⁻¹, respectively, in areas of low and moderate severity. Postfire stand density and basal area were statistically different in areas of different burn severity (P < 0.05) (Table 4). Moderate-severity fire killed many small and some larger trees, and larger trees took longer to die. Tree mortality increased significantly over time, and 3 years postfire tree mortality was 20.8% and 51.8%, respectively, in areas of low and moderate severity (Fig. 1). Three

Fig. 1. Tree mortality (bars represent SE) was higher in areas of moderate burn severity than in areas of low burn severity. Tree mortality increased over time.



years postfire live basal areas were 22.7 and 13.2 $m^2 \cdot ha^{-1}$, respectively, in areas of low and moderate severity.

We examined ~2100 live trees on study sites in low and moderate burned areas for evidence of fire-scar formation. 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. Two years postfire 99% and 88% of live trees surveyed, respectively, in low- and moderateseverity areas had crown vigor <4 (Table 2) and were rated as likely to survive. 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 areas, respectively, a difference that was statistically significant (P <0.001) ($\chi^2 = 112.9$; df = 9) (Table 5). Of trees rated likely to survive, 93% and 73% in low- and moderate-severity areas, respectively, actually survived to 3 years post-fire. Trees with incipient fire-scar formation had no significant difference (P <0.05) in percentage of circumference killed in low (34%) and moderate (38%) burn severity classes. There were no surviving trees in high-severity areas and therefore no trees with fire scars.

There were no significant differences in tree size or bark thickness between live trees with dead cambium and those with no dead cambium. Approximately 10% of all live trees had a preexisting scar or wound. Following the Jasper fire, 38% and 62% of trees with preexisting dead cambium experienced additional cambial death in low and moderate classes, respectively. Trees with preexisting scars or wounds were \sim 1.7 times more likely to experience additional cambial mortality than trees without preexisting scars.

Two years postfire, the density of tree seedlings established postfire was 530.8, 796.2, and 10.6 seedlings \cdot ha⁻¹ in areas of low, moderate, and high severity, respectively. Three years postfire, cumulative seedling densities were 612.2 and 450.3 seedlings \cdot ha⁻¹ in areas of low and moderate severity, respectively. We found no tree seedlings in high-severity areas >30 m from a patch edge. Seedling densities were not significantly different in low and moderately burned areas in either year, but differed significantly from densities in highseverity areas (Fig. 2).

Fig. 2. Postfire ponderosa pine seedlings seedling numbers (bars represent SE) were similar in areas of low and moderate burn severity, but few seedlings were present in areas of high burn severity beyond the seeding distance of ponderosa pine.



Discussion

Although the Jasper fire burned extremely fast and hot in forests long unburned (USDA Forest Service 2000), we found considerable variability in fire effects over a large area. For the 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. Approximately 60% of the to-tal acreage burned in less than 12 h. Patches of low, moderate, and high burn severity were small relative to total daily area burned and relatively evenly distributed in the landscape. Even when daily fire size was large, the ratio of daily burned area by severity class was similar to the overall proportion of burn severity represented in the landscape (Lentile 2004).

The spatial pattern of burn severity following the Jasper fire was similar to patterns described for mixed-severity fire regimes in other coniferous forests. Historical fire regimes for the Klamath-Siskiyou region of northwestern California and southwestern Oregon are generally described as mixed and dominated by low-severity components (Agee 1991; Taylor and Skinner 1998; Odion et al. 2004). Severities ranged from ~20% to 82% low, 5%-50% moderate, and 5%-45% high for large fires (>1500 ha) burning from 1977 to 2002 (Taylor and Skinner 1998). Despite drought, the effects of fire suppression, and conditions that resulted in ~100 000 ha burned during the 1987 wildfires on the Klamath National Forest, Odion et al. (2004) described a mosaic of severities (58.5% low, 29.5% moderate, and 12% high), where highseverity components were more common in recently burned areas in closed forests and in nonforest vegetation types. In contrast, high-severity fire affected ~28 000 ha, roughly half of the landscape burned by the Hayman fire, in Colorado, in 2002. Small "escapes" or narrow "tree crown streets" were embedded within large patches of crown fire in these montane ponderosa pine and Douglas-fir (Pseudotsuga menzensii (Mirb.) Franco) forests (Graham 2003). The proportion and patch sizes of high-severity fire were much smaller in Jasper than in the Hayman fire. Rather than patches of surviving vegetation within a matrix of crown fire, a matrix of surviving vegetation was interspersed with patches of crown fire in the Jasper landscape.

We saw a clear relationship between commonly examined fire evidence and burn severity following the Jasper fire. Tree mortality, incipient fire-scar formation, and tree seedling density differed significantly with burn severity. Significantly more trees died in moderate- and high-severity burns than in low-severity burns; however, to be a candidate for fire scarring, a tree must survive the fire while sustaining some degree of cambial mortality. Rates of fire-scar formation that we observed following the Jasper fire are similar to those reported by early forest researchers (Lachmund 1921, 1923; Show and Kotok 1924; Morris and Mowat 1958). However, there is little quantitative information relating to how and where fire scars are formed following wildfire (Baker and Ehle 2001). We observed a higher proportion of surviving trees with partial cambial death in moderately burned than in low-severity patches. Sherman (1969) found charred trees that did not form a subsequent scar, while Fahnestock and Hare (1964) reported that trees that initially appeared to be only charred later formed a scar. Lentile (2004) documented a higher proportion of tree basal circumference with evidence of scorched or charred bark in moderately burned than in low-severity areas. While 99% of all trees showed visual evidence of fire effects, cambial death and likely firescar formation increased in areas of moderate burn severity.

Our results did not concur with studies that found bigger trees were less likely to scar (Fahnestock and Hare 1964; Vines 1968). While larger trees are more likely to survive, we observed no differences in scarred and unscarred tree size or bark thickness in our study. Smaller trees are not likely to bear witness to the Jasper fire because most small trees died. Small trees have thin bark, low insulative properties, and increased susceptibility to complete cambial death (Fahnestock and Hare 1964; Vines 1968; Baker and Ehle 2001). Also, 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. Thus, our estimates of absolute fire-scar density in areas of low and moderate severity probably overestimate future fire-scar density, as increased physiological stress related to drought and insect attack may further reduce tree survivorship. Fire-scar densities may also be higher than what would have occurred historically given the effects of fire suppression on fuel and forest structure in these managed forests.

Several studies have shown that once a tree has scarred it becomes more likely to scar again (Lachmund 1923; Arno and Sneck 1977; McBride 1983; Johnson and Gutsell 1994). We found that trees with preexisting scars or wounds were more likely to rescar, although ~62% and 38% of trees in low and moderately burned areas, respectively, did not experience additional cambial mortality. Even with this increased likelihood of scarring, not all trees with preexisting scars will witness the Jasper fire.

What future evidence of fire will be left within the perimeter of the Jasper fire? Our results suggest that there will likely be live, old trees that predate the year 2000 over 73% of the Jasper fire area (~24 000 ha) in the central limestone region of the Black Hills. These areas of surviving forest, where burn severity was low or moderate, would form a matrix in which patches of high-severity fire had occurred. Fire scars dating to 2000 would be present on trees throughout this ~24 000 ha, in proportion to the rates of scarring and survivorship. Tree regeneration will vary considerably with direct and indirect fire effects. Following the Jasper fire, Bonnet et al. (2005) found that canopy conditions in combination with scorched needle litter and blackened mineral soil, and low herbaceous competition, explained patterns of seedling regeneration success.

In areas of low burn severity, the density of surviving trees will likely be high and fire scars will probably be present on ~20% of surviving trees. Here, closed-canopy ponderosa pine forests of large trees may persist unless they are disturbed by logging, bark beetles, fire, or additional disturbance. Although ponderosa pine seedlings can establish under a variety of tree densities, emergence into the canopy is generally limited in stands with basal area greater than $14 \text{ m}^2 \cdot \text{ha}^{-1}$ (Shepperd and Battaglia 2002). In areas of low burn severity, even after 3 years of mortality, tree basal area remained high, so that seedlings establishing postfire will be unlikely to develop as a cohort into the main canopy.

In areas of moderate burn severity, density of surviving trees will likely be low. Three years following fire, tree density was reduced by ~50% and basal areas were substantially lower relative to prefire conditions. Widely spaced, large trees form an open canopy. At least 40% of surviving trees will likely have fire scars. Basal areas have been reduced be low the threshold for canopy emergence (<14 m²·ha⁻¹) (Shepperd and Battaglia 2002). Seedlings are abundant and likely to survive and grow into the overstory, forming a dense, multiaged forest.

Two outcomes would be possible in areas of high burn severity, depending on the opening size and establishment rates. For 55% of the high severity burned area, opening size is small and most of the area is within the effective seeding distance of ponderosa pine (Shepperd and Battaglia 2002). In these openings, tree regeneration likely will be abundant, and dense, even-aged ponderosa pine stands may develop. In a companion study of spatial pattern of ponderosa pine seedling regeneration following the Jasper fire, Bonnet et al. (2005) found the highest seedling densities within severely burned patches near the edges of the unburned forest canopy. Peak seedling densities were ~1150 seedling ha^{-1} at 12 m from the unburned edge, and seedlings were found in very low densities (<100 seedlings \cdot ha⁻¹) from 40 to 180 m from an unburned edge (Bonnet et al. 2005). In areas larger than the effective seeding distance of ponderosa pine on 45% of the high-severity burn, tree regeneration has been rare, and it is likely that persistent shrub and grasslands may develop. Low seed availability and poor environmental conditions for seedling establishment were responsible for the absence of seedlings in interior regions of severely burned patches following the Jasper fire (Bonnet et al. 2005).

We believe that the forest structure created by a mixedseverity fire like the Jasper fire is consistent with the seemingly differing views of historical fire regimes for ponderosa pine forests in the Black Hills (e.g., Brown and Sieg 1996; Shinneman and Baker 1997). In one view, frequent, lowintensity surface fires maintained open stands of large, old ponderosa pine trees (Brown and Sieg 1996). This interpretation is based on sampling of fire scars in the area that was eventually burned by the Jasper fire. Alternatively, Shinneman and Baker (1997) maintain that large stand-replacing fires occurred at infrequent and irregular intervals and created large areas of dense, relatively even-aged ponderosa pine forest. This view is based on review of observations of early explorers, most prominently Graves's (1899) forest survey of the Black Hills, which also included the area eventually burned by the Jasper fire.

Fire scars were created on many surviving trees across ~73% of the affected landscape. If not taken in the context of stand structure and cohort formation, the ubiquitous presence of scars with a common date across a large area could be interpreted as widespread surface fire. While surface fire behavior did occur within the Jasper fire, surface fire alone does not adequately describe fire behavior for this event. Thus, if events such as the Jasper fire occurred in the past, these fires would not be detected by relying on fire-scar analysis alone. Frequent surface fires interspersed between less frequent mixed-severity fires such as the Jasper fire would be consistent with the fire-scar record.

Within the Jasper fire, large patches of even-aged forest will persist where there was low-severity fire, and large patches of multicohort forest will develop where there was moderateseverity fire. Some areas of high-severity fire will regenerate as even-aged forest, and some may become persistent openings. Graves's (1899) detailed descriptions of forest structure in the these large patches commonly cite multistory forest with the presence of old trees, poles, and sometimes smaller trees, with inclusions of very dense trees and grassland. For example, Graves (1899, p. 109) details the individual compartment descriptions for areas of dense forest in the area of the Jasper fire:

"A mixture of old timber about 18 inches in diameter and 60 to 70 feet height, with a clear length of 15 to 30 feet, and second-growth poles which have an apparent age of about 100 years and saplings about 40 years old. A large proportion of old trees show injury by fire at the butt. Many high flats open and covered with a thick sod of grass. At edge of timber line trees coarse and scrubby."

The forest structure created by a mixed-severity fire like the Jasper fire is consistent with the fire-history evidence developed by Brown and Sieg (1996) and with the observations of Graves (1899) as cited by Shinneman and Baker (1997). Our results are also consistent with Agee's (1998) description of mixed-severity fire regimes, where a complex mix of stand-replacement and fire effects benign to dominant vegetation occur in the same fire event. Much of the forest would have multiple cohorts present — the result of surface fire and torching associated with mixed-severity fires and intervening surface fires. Larger trees would bear fire scars from large mixed-severity events and intervening surface fire. Patches of dense trees and patches of grassland would develop where stand-replacing fire occurred within a mixedseverity event. Grass would dominate where ponderosa pine seed source was not present or where sod-forming grasses excluded pine seedlings. Dense trees would occur where a close pine seed source was available and other conditions were favorable. This comparison leads us to the conclusion that mixed-severity fire may have been common historically in the Black Hills and, in conjunction with frequent surface fire, played an important role in shaping a spatially heterogeneous, multicohort ponderosa pine forest.

Our results need to be carefully considered before using them to calibrate the relation between fire-history evidence and elements of a fire regime. Baker and Ehle (2001) criticized current interpretations of fire history based on fire-scarred tree analysis and called for 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 1994; Covington et al. 1997). Nearly all the unreserved and operable forests in the Black Hills have been harvested by partial cutting since Euro-American settlement (Shepperd and Battaglia 2002). Fire suppression in the last century has lengthened fire return intervals. Fire alone does not determine forest structure. Climate changes and other endemic and episodic disturbances (e.g., insect and disease outbreaks and windthrow) also affect forest structure and composition at multiple temporal and spatial scales (e.g., Shepperd and Battaglia 2002; Brown 2003; Hessburg et al. 2005). Current forests probably have lower structural diversity, higher tree densities, and higher surface and canopy fuel continuity, when compared with historical forests.

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