

THESIS

LONG-TERM FOREST RECOVERY PROCESSES FOLLOWING A
LARGE, MIXED SEVERITY FIRE IN PONDEROSA PINE
ECOSYSTEMS OF THE BLACK HILLS, SOUTH DAKOTA, USA.

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ABSTRACT

LONG-TERM FOREST RECOVERY PROCESSES FOLLOWING A LARGE, MIXED SEVERITY FIRE IN PONDEROSA PINE ECOSYSTEMS OF THE BLACK HILLS, SOUTH DAKOTA, USA.

Understanding the pattern and timing of ecological recovery following wildfires in western forests has become critical as the area burned has dramatically increased in the past decade. This is especially important in ponderosa pine forests, where mixed severity fires lead to a complicated landscape mosaic of initial fire effects and patterns of recovery. I compared forest structural change in relation to initial fire severity, 10-years following the Jasper Fire of 2000 in ponderosa pine forests of the Black Hills of South Dakota. The Jasper Fire burned ~34,000 ha as a mixed severity fire with 25% low, 48% moderate and 27% high severity.

I measured 43 sites within and adjacent to the Jasper fire perimeter which represented unburned areas and areas burned at low, moderate and high severity. These sites were established in 2001, immediately following the Jasper fire, and were measured annually for the first 5 years. My work constitutes the 10-year re-measurement of these sites. I assessed forest recovery as accumulation of forest floor biomass, seedling regeneration, snag dynamics, tree survivorship and growth of surviving trees.

Stand density has remained constant for unburned sites at ~25 m² ha⁻¹ since the fire, but has continued to decline in low and moderate sites which were at 18 and

9 m² ha⁻¹. After 10 years, high severity sites had 63 Mg ha⁻¹ of forest floor woody debris and were significantly greater than other burned sites and unburned sites where biomass was ~14 Mg ha⁻¹. Approximately 80% of forest floor biomass on high severity sites was coarse woody material (>7.6 cm). There was no difference in fine material (<2.5 cm) between burned and unburned sites. The difference in coarse woody debris was due to the near complete fall of snags on high severity sites where 87% of fire-killed trees have now fallen. Litter on low severity sites was similar to unburned sites but is still significantly lower on moderate and high severity sites. Duff remains ~85 to 99% less on burned sites compared to unburned sites.

Regeneration was substantial on unburned, low, and moderate severity sites. Unburned sites averaged ~6,000 seedlings ha⁻¹, while low and moderate severity sites averaged ~1,200 seedlings ha⁻¹. Regeneration was sparse on high severity sites and averaged 28 seedlings ha⁻¹, likely attributed to factors limiting seed availability. Regeneration in the first 4-5 years was low on burned sites, when the Palmer Drought Severity index averaged -1. Since 2007, the amount of surviving seedlings substantially increased, when the drought index averaged 3.5.

Tree growth measured as basal area increment for the 50 largest diameter trees per severity was significantly reduced on sites for 2001 through 2006 compared to five-year pre-fire growth. The only significant difference between severities during that time was in 2002 when moderate severity sites had higher relative growth. Growth for all sites increased in 2007 through 2010 and tree growth on moderate severity sites was significantly greater than unburned and low severity. The persistent drought from 2001 – 2006 had a more pronounced effect on tree growth than any fire effects.

Forest recovery following mixed severity wildfire is strongly influenced by initial fire effects and postfire climate. Low severity areas are similar to unburned areas in nearly all aspects of stand structure. Overstory density was substantially reduced in moderate severity areas but had increased tree growth and seedling regeneration produced a new cohort of trees that will likely lead to the development of a multi-aged forest. Regeneration in high severity areas continued to be slow, and the persistence of a sparsely treed woodland forest, or cover type conversion in some instances, is likely. Importantly, many processes of recovery have accelerated in the past 3 years, as the persistent severe drought conditions of 2001 – 2007 have subsided.

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Introduction

Ponderosa pine forests burn with fire behavior that ranges from low intensity surface fires to stand replacing active crown fires in a single event (Shinneman and Baker 1997, Baker and Ehle 2001, Sherriff and Veblen 2006, 2007, Lentile 2005, 2006, Keyser 2008), altering the postfire vegetation and forest structure in relation to burn severity (Casady et al. 2010, Keyser et al. 2008, Agee 1993). Low intensity fire behavior and associated fire effects cause less damage to vegetation and result in lower rates of overstory mortality than fire behavior of moderate intensity. Extreme fire behavior and fire effects results in complete overstory mortality and near complete removal of organic material from the forest floor. High severity fire effects may delay soil and vegetation recovery, and lead to increased severity in future fires as large woody debris accumulates (Jurgensen et al. 1997; Agee 2003). The necessity to understand the impacts and implications of mixed severity wildfires is heightened as the annual area burned in ponderosa pine forests increases (Grissino-Mayer and Swetnam 2000, Keane et al. 2002). Although numerous studies (e.g. Bonnet et al. 2005, Lentile et al. 2005, 2006, Keyser et al. 2008, 2010) have examined factors of short-term postfire recovery (1 to 5 years postfire), evaluations of forest recovery for longer periods are uncommon. This study evaluates and compares the effects of a large, mixed severity wildfire in ponderosa pine forests of the Black Hills, South Dakota, 10 years postfire to previous results from between 1 and 5 years postfire.

The Jasper Fire was ignited on August 24, 2000, and burned approximately 34,000 ha of ponderosa pine (*Pinus ponderosa* Laws.) forests during extreme weather

conditions in the central Black Hills of South Dakota before it was controlled on September 8, 2000. Small scale differences in fuel availability, topography, and stand structure (Lentile et al. 2006) resulted in a complex mosaic of mixed fire severity on the landscape with live trees remaining on a significant portion of the area (US Forest Service 2000, Lentile et al. 2005, 2006). Patches of contrasting severities were intermixed in the burned area and were comprised of approximately 25% as low severity, 48% as moderate severity, and 27% as high severity (Lentile et al. 2005). Previous research (Lentile et al. 2005, Keyser et al. 2008, 2010) within the Jasper fire indicated significant differences in forest floor biomass accumulation, seedling regeneration, and overstory survivorship, among burn severities compared to unburned forest stands in the first 5 years postfire.

The composition of biomass at the forest floor is dependent on burn severity and time since fire (Hall et al. 2006, Passovoy and Fulé 2006). Keyser et al. (2008) found significant decreases in litter and duff among all burn severities immediately following the Jasper Fire. Litter, duff, fine woody debris (FWD), and coarse woody debris (CWD) were initially reduced in all burned areas. Litter was initially reduced by 68, 88, and 92% in areas that burned as low, moderate, and high severity compared to 16.1 Mg ha⁻¹ in unburned areas. Duff followed similar reductions and low, moderate, and high severity areas were 89, 95, and 98% lower than unburned areas which contained ~28 Mg ha⁻¹. Compared to unburned areas which contained 5.9 Mg ha⁻¹, FWD was reduced by 64, 80, and 92% in areas that burned under low, moderate and high severity, respectively. The amount of CWD in areas that burned as low, moderate, and high severity was reduced

by 83, 86, and 81% compared to unburned areas that contained 14.0 Mg ha⁻¹ (Keyser et al. 2008).

Litter and duff remained lower in burned areas compared to unburned areas 5 years postfire, although abscised scorched needles contributed to litter accumulation in areas where the overstory was not fully consumed in the fire. Areas that burned as low and moderate severity had accumulated litter amounts 25 and 36% lower than unburned areas. High severity areas had no litter accumulations and remained 93% lower than unburned areas, which contained 16.3 Mg ha⁻¹. Duff increased minimally in low and moderate severity areas but they remained 78 and 84% lower compared to unburned areas that contained 25.2 Mg ha⁻¹.

By 2005, FWD in moderate and high severity sites was not different from amounts in unburned sites. CWD in moderate severity sites was not different from unburned sites in 2005, but high severity sites had 30.0 Mg ha⁻¹ compared to 17.2 Mg ha⁻¹ in unburned sites. Low severity sites had significantly less FWD and CWD on the forest floor than unburned sites 5 years postfire and those reductions were expected to continue. Five years postfire, areas that burned as low severity had ~60% as much FWD and CWD compared to unburned areas. It was unclear how moderate and high severity sites would be affected after 5 years postfire as many fire killed snags had not fallen to the ground yet. Established snag fall rates following prescribed fire and fire with >50 % overstory mortality in ponderosa pine forests of the Southwest show 61 to 75% of total snags fall to the forest floor between eight to ten years postfire (Harrington 1996,

Passovoy and Fulé 2006), however it is unclear if these rates apply to Black Hills ponderosa pine forests.

Postfire seedling regeneration is influenced by many factors including proximity to seed source, forest floor conditions, overstory density, time since fire, and climatic conditions. Within the Jasper Fire, seedling regeneration was significantly higher in unburned areas compared to all burn severities 5 years postfire. Low and moderate severity sites averaged approximately 2000 seedlings ha⁻¹ and high severity sites had almost no regeneration (Keyser et al 2008). Postfire seedling regeneration is dependent upon seed availability which is influenced by canopy density, and variability between seed production years (Shearer and Schmidt 1970, Barrett et al. 1983, McDonald 1992, Shepperd et al. 2006, Keyes and Maguire 2007). Large, more vigorous trees produce more significant cone crops (Fowells and Schubert 1956, Sundahl 1971, Foiles and Curtis 1973) and indicate seed availability may not be influenced solely by stand density. Bonnet et al. (2005) determined initial densities of germinates within the Jasper Fire were higher in severely burned areas in close proximity to unburned areas compared to unburned areas. The number of seedlings decreased with distance from seed source. However, they concluded that seed availability was not solely responsible for seedling regeneration and identified other environmental factors beneficial to seedling germination that included burnt litter on mineral soil.

Areas of high severity fire rely on external patches of live overstory for ponderosa pine seed production and are affected by patch size. Fifteen percent of the high severity patches were <1 ha in size but patches ranging from 10-100 ha and 100-

1000 ha comprised 38% and 30% of the area impacted by high severity fire effects (Lentile et al. 2005). Average maximum seed dispersal distances for ponderosa pine are between 75 to 100 meters from a seedtree (Barrett 1966) and 89% of the total seed falls within a proximity of 61 meters (Barrett 1966). Others have shown up to 8% of ponderosa pine seed may fall a maximum distance of 120 meters from a seed tree (McDonald 1980, Oliver and Ryker 1990, Bonnet et al 2005). Savage and Mast (2005) report that up to 50 % of the 6180 ha burned as a stand replacing fire in Southwest ponderosa pine forests was converted to meadow and regeneration occurred only along live edges providing a seed source.

Climatic factors also have a substantial effect on seedling establishment in the Black Hills and all previous research within the Jasper Fire was conducted during extended drought conditions. Ponderosa pine germinates rely heavily on adequate moisture for survival (Savage et al. 1996, Shepperd et al. 2006). Brown (2006) correlated historical germination success and seedling survival in the Black Hills with extended periods of increased moisture. The climatic conditions of increased moisture during the growing season described by Brown (2006) to favor seedling regeneration were absent in the first 7 years following the Jasper Fire. However, in the past 2 years, drought conditions have relaxed and may favor germination success and survival. These favorable climatic conditions should provide insight into the impact fire severity has on seedling germination in the absence of drought.

Growth response of remaining overstory trees following a wildfire provides a more complete analysis of the effect of different burn severities on postfire tree health

and vigor, which has numerous management implications. Few studies have examined mid to long-term prescribed fire effects on tree growth (Sala et al. 2005) and fewer yet have examined the effects of wildland fire on tree diameter growth. Previous research (Keyser et al. 2010) from the Jasper Fire failed to detect any differences in radial growth in 4 of the first 5 years postfire between unburned and burned areas of low and moderate severity. However, the prior study was conducted during a time of extended drought which began the year of the Jasper Fire. The effects of the drought were unknown and long-term changes in climatic conditions have the possibility of influencing growth rates and overstory response.

Most studies that examine the growth response of overstory trees after prescribed and wildfire are confounded by stand density reductions implemented before the fire. For example, Pearson et al. (1972) found that wildfire effects resulted in a positive growth response where annual increment widths substantially increased after crown losses <50% and modestly increased for all trees with crown damage <85%. However, these results were from a recently thinned stand of ponderosa pine and fire effects were not isolated within that study as a result of the design. Other studies have concluded that growth is reduced (Landsberg et al. 1984, Grier 1989, Sutherland et al. 1991, Landsberg 1992, Busse et al. 2000) or increased (Skov et al. 2005, Sala et al. 2005) with the application of prescribed fire. Studies where positive growth effects were observed after prescribed fire also underwent prefire density thinning operations and increased growth was found in thinned stands without fire. Other studies found no

significant relationship between growth reduction and stand density in prescribed burned stands 6 to 8 years postfire (Sutherland et al. 1991, Busse et al. 2000).

Postfire planning is an important element in controlling the considerable monetary and ecological costs associated with postfire restoration and management. Long-term monitoring of the Jasper Fire provided a unique opportunity to study and compare postfire ecological processes through time, between fire severities, and different climatic conditions. This study evaluates the necessity of long-term forest recovery studies by analyzing and comparing the accumulation of forest floor biomass, seedling regeneration, and overstory survivorship and growth response 10 years after a large, mixed severity wildfire in ponderosa pine forests of the Black Hills, South Dakota, to results from the first 1 to 5 years postfire. I hypothesize that the time elapsed since 5 years postfire and changing climatic conditions will result in:

1. Constant litter amounts in all unburned and burned severities with an increase of duff in low and moderate severity sites.
2. Increased FWD and CWD in moderate and high severity sites while low severity sites maintain reductions as a result of the fire.
3. Increased seedling regeneration in unburned, low, and moderate severities with a persisting lack of regeneration in high severity sites.
4. Stabilization of overstory mortality in all sites where an overstory is present.
5. Increased diameter growth in moderate severity sites, compared to unburned and prefire growth, as a result of initial stand density reduction with unchanged growth in low severity sites.

Methods

Study Area

This study was conducted within and immediately adjacent to the Jasper Fire perimeter located in the Black Hills, South Dakota, USA. The Jasper Fire was ignited on August 24, 2000, and burned approximately 34,000 ha of ponderosa pine (*Pinus ponderosa* Laws.) forests during extreme weather conditions in the central Black Hills of South Dakota before it was controlled on September 8, 2000. Small scale differences in fuel availability, topography, and stand structure (Lentile et al. 2006) resulted in a complex mosaic of mixed fire severity on the landscape with live trees remaining on a significant portion of the area (US Forest Service 2000, Lentile et al. 2005, 2006). Patches of contrasting severities were intermixed in the burned area and were comprised of approximately 25% as low severity, 48% as moderate severity, and 27% as high severity (Lentile et al. 2005). Patch sizes in low and moderate severities were concentrated between 100-1000 ha (38%) and greater than 1000 ha (30+%) while high severity was largely composed of patches 10-100 ha (38%) and 100-1000 ha (32%) with no recorded patches 1000 ha or greater (Lentile et al. 2005).

The Black Hills were formed by an isolated uplift rising from the surrounding Great Plains Province and extend 125 miles north to south and 60 miles east to west (Hoffman and Alexander 1987). Elevation ranges between 1500-2100 m within the study perimeter. Climate is continental (Johnson 1949) with cold winters and warm, moist summers. There is a strong precipitation gradient from north to south, where

precipitation averages 74 cm in the north but only 41 cm in the south (Driscoll et al 2000). 65-75% of the precipitation occurs between the months of April and October (Hoffman and Alexander 1987, Froiland 1990, Shepperd and Battaglia 2002). Precipitation for study sites was calculated by overlaying site coordinates with geospatial data obtained from The Prism Climate Group. Site specific annual precipitation averages from 48.6 cm to 63.8 cm, and increases from south to north and west to east within the study area. The highest precipitation occurred along the ridge of the Limestone Plateau (Shepperd and Battaglia 2002). Soils within the fire perimeter were Alfisols, Mollisols, and Inceptisols (Shepperd and Battaglia 2002) and did not vary from adjacent areas.

Experimental Design

In 2010, I re-measured the plots established immediately following the Jasper Fire in the spring of 2001, as described by Keyser et al. (2008). Sites were categorized into burn severities using Ryan and Noste's (1985) classification system (Table 1). I measured an additional 9 high severity sites which were not previously reported. High severity sites were apportioned so 9 sites each were located 50 and 150 meters from an existing live seedsource. All measurements within high severity sites were averaged when compared to results from 2001 through 2005. A total of 7 unburned sites were used for baseline comparisons because two sites were harvested between 2005 and 2010. Unburned sites were located in close proximity to the fire perimeter. Using sites outside of the fire perimeter for baseline comparisons has been employed in numerous

other studies (e.g. Prichard et al. 2010, Fulé and Laughlin 2008, Fulé et al. 2004) and is a reasonable proxy for pre-fire control units. Keyser et al (2008) found no significant differences in prefire stand structure between unburned sites and any burn severity used in this study.

Overstory Tree Measurements

Three circular 0.03 ha overstory plots were constructed 20m from site center at 0, 135, 225 degrees at each site in 2001 (Figure 1). Individual trees within each overstory plot were tagged when initial tree data was recorded. Initial measurements consisted of diameter at breast height (DBH, 1.4m), total height (HT), height to live crown (HLC) and height to lowest live branch (HLB) each measured where the branch meets the bole,. Measurements were repeated in 2005 (Keyser et al. 2008).

In 2010, I re-measured DBH, HT, HLC, and HLB with the addition of bark thickness (BARK) taken at two points separated by 90° on the bole at breast height (1.4 m) for each live tree. Heights for all standing and broken snags were also measured. Live trees were cored at breast height and were selected without bias to any features by using a coring ratio in each site as follows: 0-25 live trees = 1:1, 25-50 live trees = 1:2, 50-75 live trees = 1:3, 75-150 live trees = 1:4, 150+ live trees = 1:5. Cores were stored in paper straws until processed. Increment widths were measured to the nearest .01 mm in a laboratory using a microscope and a linearly controlled stage and microscope attached to a digital encoder (Velmex Inc).

Woody Fuels and Forest Floor Measurements:

I measured fine woody debris (FWD) (<7.6 cm) and coarse woody debris (CWD) (>7.6 cm) along three, 30 meter transects using Brown's planar intersect method (Brown et al. 1982). Transects originated at each overstory plot center and continued outward along the bearing from site center (Figure 1). One (<0.635 cm) and 10 hour (0.635 – 2.54 cm) fuels were sampled over 6 m, 100 hour (2.54 – 7.62 cm) fuels over 9 m and 1000 hr (>7.62cm) over the entire transect length (sensu Brown et al. 1982). Duff and litter depths were measured on the transect at three points. Depths were converted to mass using bulk densities for pine litter (60.7kg/m³) and duff (102.6kg/m³) specific to the Black Hills (Battaglia et al. 2008).

Tree Regeneration

Tree regeneration was measured in each site on 30, 28.3 m² plots on an 80x80 m grid randomly oriented about the site center (Figure 2). Plots were located within the grid at 20x16 m spacing. Seedlings were tallied by height classes of 1-5 cm, 5-10 cm, and then by 10 cm intervals to a maximum height of 1.4 m. Current germinates were not counted.

I sampled 10 seedlings in each of 21 sites across unburned, low, and moderate severities to establish a relationship between seedling height and age. Ten defect free seedlings per site were harvested outside the 80x80 m seedling measurement grid. Seedlings were harvested from similar conditions to where the measurement grid was placed, including aspect, slope, and canopy cover. Seedlings were harvested from a site if a minimum of ten seedlings were tallied in abundance measurements and if the

adjacent areas appeared reasonably stocked with regeneration. Each seedling was measured for total height and a cross section was cut at the root collar for accurate age determination.

Statistical Analysis

Measurements of increment growth, FWD and CWD, duff and litter mass, and basal area losses through mortality were tested for differences between low, moderate, and high severities using a one-way analysis of variance (ANOVA) in SAS (SAS Institute 2008). Individual ANOVA tests were performed for all fuels size classes. ANOVA tests were performed separately for each year (1995-2009) to analyze differences in basal area increment (BAI) and relative BAI growth between unburned sites and burn severities. Response variables were log or fourth root transformed to approximate normality and homoscedasticity if necessary. All ANOVA tests were performed at the $\alpha=.05$ significance level using Tukey's HSD adjustment. Means and standard errors reported are from non-transformed data. Due to changes in sampling design for seedling regeneration and forest floor biomass, a repeated measures analysis was inappropriate for comparing to results from 2001 through 2005. As such, non-statistical comparisons are made to earlier results.

Development of a seedling height to age relationship was performed by fitting an analysis of covariance (ANCOVA) generalized linear model to the data (SAS Institute 2008). Terms contained in the model included "severity" as indicator variables,

“height,” and an interaction term of “height x severity”. All seedling height inputs were fourth root transformed.

I compared seedling abundance between severities by performing a Multiple Response Permutation Procedure (MRPP) as described in Biondini et al. (1988). MRPP is an F-based test not constrained by the typical assumptions of normality and equal variance, and is robust against outliers. MRPP plots data on Cartesian coordinates and analyzes groups of data (i.e. severities) based on within-group Euclidian distances and between-point Euclidian distances for all data.

Postfire tree growth was compared across time and severities through basal area increment (BAI) and relative BAI. Relative BAI is a unitless value that represents a change in annual BAI proportional to pre-fire growth patterns (Keyser et al. 2010, Skov et al. 2005) and has been utilized in other growth studies (Salonius et al. 1982, Reinhardt and Ryan 1988, Keyser et al. 2010). Relative basal area compares five years pre-fire average BAI growth to individual years postfire. Values between zero and one indicate a growth decrease and values above one indicate a positive growth response over pre-fire conditions. BAI was linearly regressed against the Palmer Drought Severity Index (PDSI) for the 50 largest diameter trees per severity.

I determined the year of germination for seedlings by fitting the data from 178 destructively sampled seedlings to an analysis of covariance (ANCOVA) regression model which included terms for “severity”, “height”, and a “height x severity” interaction. The model was fit using seedlings ten years of age or less in low and moderate severities due

to the change of growing conditions subsequent to the fire and the probability of stunted growth from damage to seedlings that survived. Twenty-seven% of the seedlings aged in low severity sites had ages in excess of ten years and 20% were older than ten years in moderate severity sites. Seedling data in unburned, low, and moderate severities were fit to the model:

$$y_{ij} = \mu + \alpha_1 + \alpha_2 + \beta(x) + \gamma_1(x) + \gamma_2(x) + \epsilon_{ij}$$

where y_{ij} is the estimated age of the seedling in 2010, μ is the intercept for moderate severity and β is the slope parameter for height in moderate severity. Parameter α_1 is the intercept adjustment for baseline and α_2 for low severity. Adjustments to the slope by parameters γ_1 and γ_2 are for baseline and low severity respectively which result from the interaction between height and severity. Error in the model (ϵ_{ij}) has no effect because the sum of residuals from the output is zero. Height values in the model are input as X and are in the form of the fourth root transformation. Model fit resulted in an R^2 of 0.8603 over the entire model and all terms (“severity,” “height,” “height x severity” interaction) used in the model are significant ($p < .0001$). Values for model parameters and fit characteristics are shown in Table 2. All high severity sites lacked the seedlings necessary to destructively sample or fit a model for predicting age by height. The seedling age model was used to estimate the year of germination for the 5535 seedlings measured in regeneration plots. The heights input to determine seedling age were median values for each size class used in regeneration abundance plots.

Results

Pre-fire stand structure in the study area was described by Keyser et al. (2008) as even-aged, second growth, pure, ponderosa pine forests which were well stocked with an average stand diameter (ASD) of ~22 cm, and an average ~24 m² ha⁻¹ BA with ~670 stems per hectare. Mortality since 2005 resulted in average basal area losses of 0.97, 2.29, and 0.99 m² ha⁻¹ in unburned, low, and moderate severities (Figure 3). In 2010, unburned sites had an ASD of 17.2 cm and an average BA of 24.9 m² ha⁻¹. Stand structure in low and moderate severity sites consisted of an ASD of 23 cm and 18.2 m² ha⁻¹ BA in low severity sites and an ASD of 27 cm and 9.3 m² ha⁻¹ BA in moderate severity sites. Unburned, low, and moderate severity sites had an average of 883, 565, and 221 stems per hectare. Standing snags averaged 14, 54, 8, and 5 per hectare in unburned, low, moderate, and high severities respectively (Figure 4). In high severity sites, 87 % of snags which resulted from initial mortality had completely fallen to the forest floor and another 12.6% had broken along the bole which left less than half a percent standing.

Forest Floor

CWD was significantly different among severities ($F=37.47$ $p<.0001$) and was reduced on low severity sites compared to other burned sites but high severity sites exceeded unburned amounts. Unburned and moderate severity sites were not significantly different despite an accumulation of CWD in areas that burned as moderate severity. Sites burned at high severity resulted in CWD amounts significantly above

unburned sites (Table 3). CWD on high severity sites was approximately 6 times that of unburned. The average CWD load in high severity sites was approximately 50 Mg ha⁻¹. CWD in sites where fire occurred were dominated by solid, non-decayed logs. Rotten logs in low severity comprised only 3% of the total, 17% of the total was rotten in moderate severity, and an average of 10% of the total CWD load was rotten in high severity sites. Rotten logs in unburned sites averaged ~6 Mg ha⁻¹ and accounted for 54% of the CWD total.

No substantial differences existed between any unburned or burned severities for fine woody debris (FWD). FWD was not significantly different in any fuel size class apart from the 100 hour fuels class (Table 3). High severity sites 50 meters from live trees had significantly greater accumulations of FWD than low and unburned sites (F=10.42 p<.0001).

Duff was significantly lower in all burned sites compared to unburned sites (F= 22.58 p<.0001). Unburned sites averaged 26.5 Mg ha⁻¹ of duff. Duff was reduced by >85% on low and moderate severity sites compared to unburned sites, and averaged <4 Mg ha⁻¹. High severity sites averaged <0.2 Mg ha⁻¹ and had duff reductions of > 99% compared to unburned sites. Litter was similar on unburned and low severity sites but was significantly reduced (F= 17.35 p<.0001) on moderate and high severity sites compared to unburned sites. Litter was decreased by 55% in moderate severity sites compared to unburned sites (Table 3). High severity sites were significantly lower than all other severities and decreased by 81% compared to unburned sites (Table 3).

Tree Regeneration

Postfire seedling regeneration was significantly lower in all burned sites compared to unburned sites (Table 4). Unburned sites averaged 6023 seedlings per hectare (Table 4). Low and moderate severities had significantly less regeneration than unburned sites, but were well populated with seedlings and averaged approximately 1200 seedlings per hectare. Seedling regeneration was low on high severity sites with 38 seedlings per hectare at 50 m from live edge and 18 seedlings per hectare at 150 m. There were considerable differences between high severity sites and no seedlings were present on southern sites near Jewel Cave National Park.

Postfire seedling establishment was slow in low and moderate severity areas for the first 6 years following fire (Figure 5). Seedling regeneration increased between 7 and 9 years postfire and accounts for more than 50 % of the total seedlings in low and moderate severity sites. Seedling regeneration 7 to 9 years postfire totals ~700 seedlings ha⁻¹ in low and moderate severity sites.

Overstory Growth Response

Diameter growth within burned severities was significantly correlated with PDSI (Table 5) and burned severities produced larger BAIs for each increase in PDSI (Figure 6). Each severity was fit separately after analysis of the PDSI x Severity interaction was significant at the 95% confidence limit. Comparing only the 50 largest diameters from each severity reduced the effects of suppressed and non-dominant trees on BAI. The average DBH of the 50 largest trees in unburned sites was 32.3 cm (26 cm min. 60.5 cm

max.), 33.8 cm in low severity (27.7 cm min. 49.4 cm max.), and 32.4 cm in moderate severity (27.5 cm min. 45.9 cm max.).

Growth response evaluated as relative BAI for the 50 largest diameter trees per severity resulted in significant differences within years and across severities (Figure 7). Significant differences in relative BAI existed in 2002 ($F=3.17$ $p=.0447$) when moderate severity sites were significantly higher than unburned, in 2008 ($F=4.38$ $p=.0142$) when moderate severity sites were significantly higher than low severity, and again in 2009 ($F=3.79$ $p=.0248$) when moderate severity sites were significantly higher than unburned sites. All severities recorded a mean relative BAI below 1.0 until 2008 when moderate and unburned sites measured 1.173 and 1.003, and in 2009 when moderate sites measured a relative BAI of 1.18.

Discussion

This study evaluated the accumulation of forest floor biomass, seedling regeneration, overstory survivorship, and growth response as key factors of long-term forest recovery, with respect to different burn severities, time, and postfire environmental factors, to answer if long-term postfire recovery studies are warranted. Recovery rates differed among burn severities during the first 5 years postfire (Keyser et al 2005, Lentile 2006) but some results were confounded by environmental conditions and questions remained with regard to other long-term recovery processes. Results from 10 years postfire indicated long-term changes in forest recovery stemming from initial fire effects and a shifting postfire climate.

Overstory mortality attributed to fire effects had the most significant influence on stand structure during the first five years postfire but held implications for forest floor recovery ten years postfire. The forest structure after 5 years postfire remained in place 10 years postfire. No substantial mortality of overstory trees occurred between 2005 and 2010 and low and moderate severities had mortality rates similar to unburned sites (Figure 8). However, the input of woody material, which resulted from initial mortality, affected recovery of the forest floor 10 years postfire. Initial benefits from low and moderate severity fire included woody biomass reductions congruent with fuels management objectives. Conditions within these stands at 10 years postfire were no longer in line with those objectives. Changes in litter (Figure 9), FWD (Figure 10), and CWD (Figure 11) between 2005 and 2010 resulted in a woody fuels complex that is not different from unburned areas ten years postfire. Low severity sites contained substantially more standing snags than all other unburned and burned severities (Figure 4) and further contributions of woody biomass should be expected (Passovoy and Fulé 2006, Thies et al. 2006) in these areas. Woody debris in areas that burned as moderate severity was near the recommended maximum for ponderosa pine forests (Harvey et al 1987, Graham et al 1994). The complete mortality of overstory trees in high severity areas created the potential for excessive amounts of woody fuels on the forest floor. Although woody fuels accumulations during the first 5 years postfire did not pose a concern for future re-burn events, the fall rates for snags in the Black Hills exceeded those observed in southwest ponderosa pine forests at ten years postfire (Harrington 1996) and the accumulation of CWD now presents a hazard situation

(Brown et al. 2003) for fire behavior and severe fire effects (Frandsen and Ryan 1986, Hartford and Frandsen 1992, Knapp et al 2005, DeBano et al. 1998) as a result of increased fire resonance time (Kauffman and Martin 1989, Giacomo 2005). Duff had minimal additions over the entire 10 year study period and the recovery of a substantial duff layer will be slow (Figure 12).

Overstory growth response of remaining live trees was more influenced by postfire climate conditions than by any fire effects, such as crown damage. Persistent drought conditions were likely a confounding factor in previous growth studies (Keyser et al. 2010) within the Jasper Fire area. As the drought subsided, dominant trees that survived in moderate severity sites were the only trees that repeatedly produced diameter growth above pre-fire increments. These trees may have benefited from increased water potential (Skov et al. 2004, 2005) and decreased competition for resources. Dominant trees located in low severity sites were slower to respond to improved climate conditions and never attained growth equal to pre-fire amounts, although postfire climate was still the dominant factor. This is consistent with other short-term studies that concluded density was an integral factor to postfire growth following prescribed burns (Sutherland et al 1991, Covington et al 2001) and agrees with others that have concluded decreased growth following prescribed burns (Landsberg et al. 1984, Grier 1989, Sutherland et al. 1991, Landsberg 1992, Busse et al. 2000).

Tree seedling establishment was controlled by drought factors and was abundant ten years postfire in areas that burned as low and moderate severity. Low

and moderate severity sites averaged ~ 1200 seedlings ha^{-1} and exceeded fully stocked amounts of regeneration, despite being significantly lower than unburned sites. The number of seedlings present 10 years postfire was substantially lower than the maximums of almost 8000 and 4000 ha^{-1} (including germinates) observed by Keyser et al (2008) during the first 5 years postfire in low and moderate severity sites, respectively. Survivorship of postfire germinates was likely limited by persistent drought conditions (Bihmidine et al. 2010) and may account for the inconsistent seedling counts between each year during the first 5 years. Approximately 50% of the established seedlings in low and moderate severity sites germinated between 7 and 9 years postfire, which coincided with the subsidence of drought conditions. The Black Hills provide a favorable growing climate for seedlings and extensive regeneration is predicted in these areas given the continuance of typical, non-drought precipitation and temperatures. However, a different future is likely for areas of high severity as tree regeneration was highly variable, but generally deficient in all sites throughout the entire ten year period. Regeneration was not significantly different between high severity sites 50 m and 150 m from a seedsource and averaged 28 seedlings ha^{-1} . Sampling in the southern region of the Jasper Fire failed to detect any seedlings, which agrees with previous findings by Mitchel and Yuan (2010).

Future management may prove most beneficial in areas that burned as low severity given that these areas have retained the majority of the overstory basal area and hold the greatest possibility for timber production or loss. Woody debris accumulations combined with extensive seedling regeneration acting as ladder fuels

(Battaglia et al. 2008) and a live crown base height that was not significantly raised in the fire could result in extreme fire behavior during wildfire conditions. Prescribed fire operations in these stands will yield gradually lower seedling mortality as seedlings increase in size (Battaglia et al. 2009). Without management, these areas will continue to contribute to the Black hills timber base but the fire hazard will increase with additional inputs of woody debris and seedling regeneration.

Postfire stand structure resembled a shelterwood type of silvicultural operation and overstory recovery is occurring in areas that burned as moderate severity. Seedling regeneration has been successful and will produce multi-storied stands. Woody biomass at the forest floor did not substantially accrue between 2005 and 2010 and future considerable accumulations are not expected. These areas will remain at low risk for crown fire due to the significantly raised canopy base height (Keyser et al. 2008), despite successful seedling regeneration and the accumulation of woody debris. Typical management actions will apply to these areas as recovery progresses towards typical Black Hills stand structure in the future.

Areas that burned as high severity had the greatest departure from prefire structure and the results from 10 years postfire provide a reference for management and planning. Woody fuels accumulations during the first 5 years postfire did not pose a concern for future re-burn events and opportunities for management in high severity areas were limited 5 years postfire (Keyser et al. 2008). However, almost no snags remain standing 10 years postfire and the composition of woody fuels will persist on the

landscape if no actions are taken to reduce the hazard. Only ~10% of the CWD in high severity sites was classified as rotten which may hinder desirable amounts of consumption (Brown et al. 1985, Kauffman and Martin 1989) in prescribed fire without burning under hot and dry conditions. The CWD in these areas will become more available for ignition as the dominant decay class shifts from sound to rotten and may be expected between 11 and 20 years postfire (Passovoy and Fulé 2006, Battaglia et al. 2008). Seedling regeneration was deficient in all areas that burned as high severity despite the subsidence of drought conditions and a rapid recovery to forested conditions is not probable. Without planting efforts these areas are likely to persist as sparsely forested woodlands or, in the case of the southern region, as grass/shrub cover types. If returning these areas to timber producing forests is the desired result, then planting may be the only means of accomplishing the goal. However, these areas offer a unique refuge for wildlife (Hill 1946, Harmon 1986, Deperno et al. 2002) and introduce heterogeneity in an otherwise homogenous landscape.

Variable rates of recovery following mixed severity fires can present unique challenges to land managers aimed at forest management and restoration. Variable rates of recovery with respect to different burn severities will continue to perpetuate a heterogeneous landscape beyond 10 years postfire. This study provides managers valuable information regarding long-term recovery processes, which not available immediately following the Jasper Fire, and highlights the need for long-term studies within the Jasper Fire and other similar disturbance events. The results from this study

support the variable nature of mixed severity fire and illustrate the need to perform postfire management and restoration on a stand level basis.

Table 1. Fire severity classes applied to fire behavior in ponderosa pine stands that occurred during the Jasper fire of 2000, in the Black Hills, South Dakota. Severity classes follow Ryan and Noste's (1985) classification system and have been utilized in previous studies of the Jasper fire (Lentile et al. 2005, 2006 Keyser et al. 2006, 2008, 2009, 2010).

Fire severity class	% of Landscape	Associated fire behavior	Fire behavior indicators
Unburned	N/A	N/A	Study sites were located in unburned stands adjacent to burned sites and serve as reference for basis of forest recovery
Low	25	Surface fire	Partial consumption of litter and duff with no exposed bare mineral soil, Crown scorch <25% with no crown consumption
Moderate	48	Surface fire with individual tree torching	Consumption of the majority of litter and duff and >25% crown scorch with some crown consumption
High	27	Stand replacing active crown fire	Complete consumption of litter and duff, crown foliage, and 100% overstory mortality

Table 2. Seedlings grew at significantly different rates among burn severities and each severity had a separate curve fit to determine age from seedling height. This model was used to determine at which points seedlings established postfire and the number per hectare. Model terms are followed by (Pr>t) and parameter estimates are followed by (standard error). Model achieves an R² value of 0.8603.

Height to Age Model Inputs							
Severity	μ (0.0172)	α_{\square} (<.0001)	α_{\square} (0.1523)	β (<.0001)	γ_{\square} (<.0001)	γ_{\square} (0.0361)	ε
Unburned	0	-12.2836 (2.02)	0	0	7.8748 (0.86)	0	0
Low	0	0	-2.8022 (1.95)	0	0	1.8995 (0.9)	0
Moderate	-3.4916 (1.45)	0	0	4.1706 (0.63)	0	0	0

Table 3. Forest floor biomass as Mg ha⁻¹ by size classification and reported as the mean and (Std. error). FWD (0-7.62 cm) had few differences in any size class among different severities. CWD was significantly different among severities and high severity sites contain substantial accumulations. Means followed by differing letters indicates a significant difference at $\alpha=.05$ using Tukey's multiple comparison adjustment.

Severity	One Hour (0-0.64cm) <i>p</i> =.2229	Ten Hour (0.64-2.54cm) <i>p</i> =.3217	Hundred Hour (2.54-7.62cm) <i>p</i> <.0001	CWD (>7.62cm) <i>p</i> <.0001	Total Downed Woody Debris <i>p</i> <.0001	Litter (Mg/ha) <i>p</i> <.0001	Duff (Mg/ha) <i>p</i> <.0001
Unburned	0.17 (0.02) ^A	1.87 (0.26) ^A	4.21 (0.68) ^A	8.18 (3.18) ^{AB}	14.43 (3.81) ^A	15.13 (1.16) ^A	26.5 (3.7) ^A
Low	0.18 (0.03) ^A	1.78(0.91) ^A	3.31 (0.88) ^A	6.98 (2.09) ^A	12.58 (3.61) ^A	11.95 (1.5) ^{AB}	3.93 (1.14) ^B
Moderate	0.34(0.07) ^A	2.95 (0.56) ^A	5.79 (1.14) ^{AB}	22.78 (4.72) ^B	31.56 (4.82) ^A	6.82 (0.76) ^B	1.84 (0.56) ^B
High 50m	0.29(0.05) ^A	3.11 (0.33) ^A	11.07 (1.17) ^B	48.21 (3.30) ^C	62.67 (3.96) ^B	2.89 (0.47) ^C	0.19 (0.13) ^C
High 150m	0.28 (0.05) ^A	2.93 (0.47) ^A	8.45(1.15) ^{AB}	52.36 (3.58) ^C	64.36 (4.03) ^B	2.74 (0.39) ^C	0.13 (0.13) ^C

Table 4. Although low and moderate severity sites have significantly fewer seedlings ha-1 than unburned sites, they exceed fully stocked and will likely develop into dense multi-storied forests. Substantial variation exists within severities and some high severity areas may persist as grass/shrub cover types. Means followed by different letters are significantly different at the 95th % confidence level using the Multiple Response Permutation Procedure.

Seedlings per hectare				
Severity	Mean	Std. Error	Min	Max
Baseline	6022.63 ^A	3004.18	518.72	23708.19
Low	1253.59 ^B	393.83	82.52	3289.2
Moderate	1209.05 ^B	349.06	117.89	3336.36
High 50m	37.99 ^C	14.54	0	106.1
High 150m	18.34 ^C	8.81	0	82.52

Table 5. Parameter estimates for linear regression of BAI on PDSI for unburned, low, and moderate severities.

Regression model parameters for BAI on PDSI			
Severity	Intercept (<i>p</i>)	Slope (<i>p</i>)	R ²
Unburned	4.787 (<.0001)	0.248 (.0791)	0.38
Low	5.174 (<.0001)	0.359 (.0037)	0.72
Moderate	6.472 (<.0001)	0.613 (.0014)	0.79

Figure 1. Diagram of site design including overstory plot location, fuels sampling transects, and site center. Diagram is not drawn to scale.

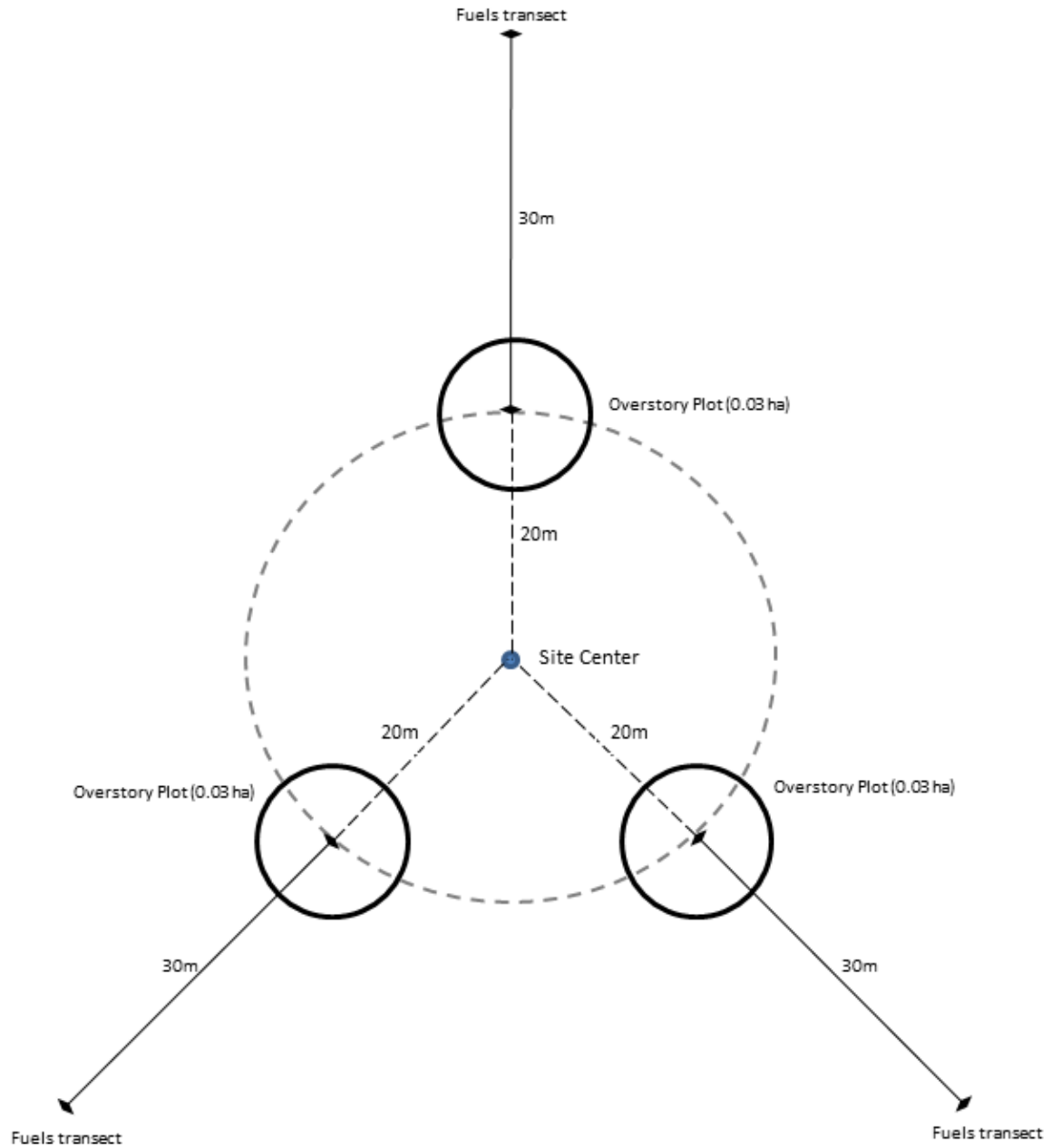
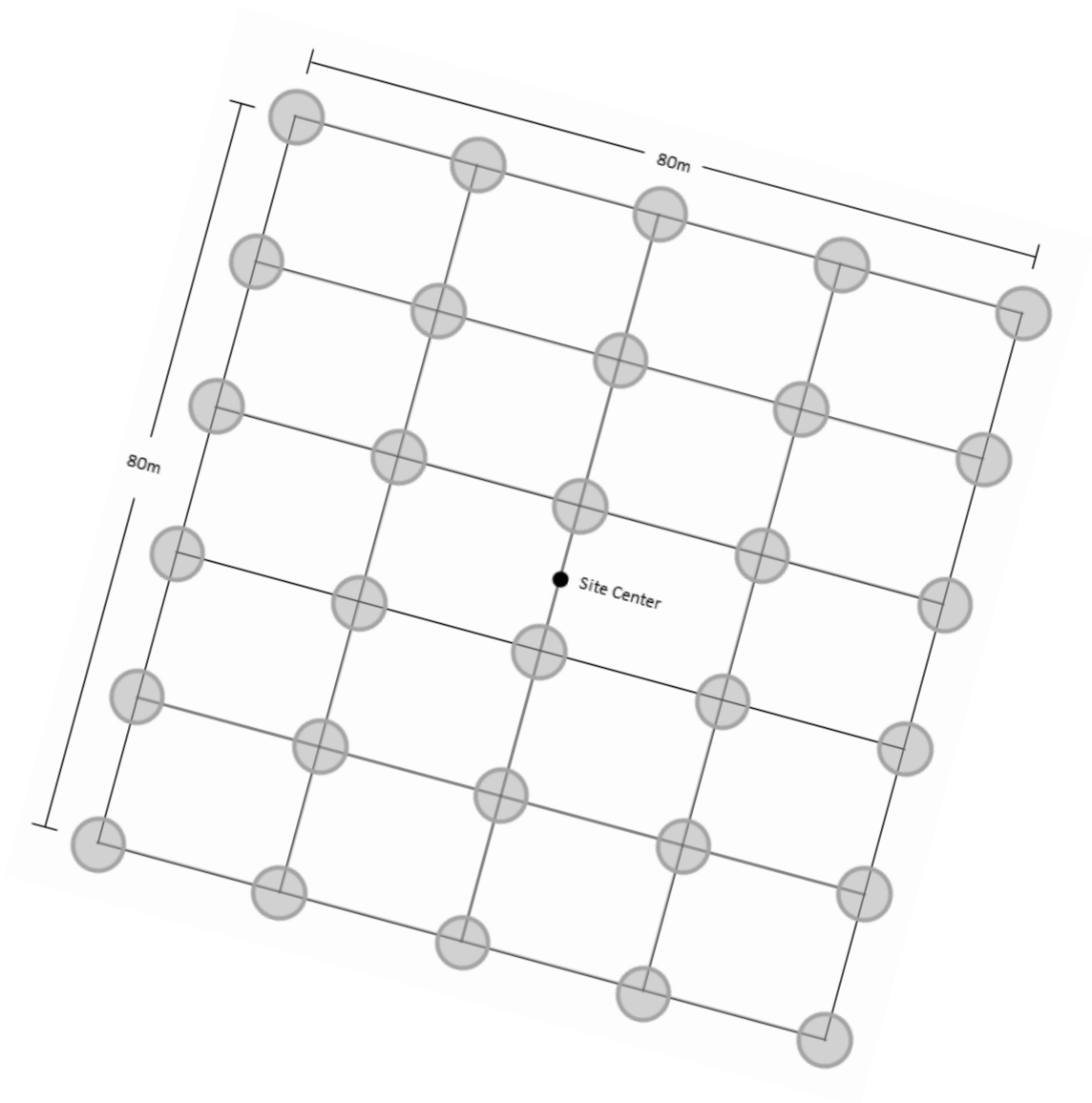


Figure 2. Diagram of seedling regeneration abundance measurement plots including site center and outer dimensions. Tree regeneration was measured in each site on 30, 28.3 m² plots on an 80x80 m grid randomly oriented about the site center. Plots were located within the grid at 20x16 m spacing.



Mortality Between 2005 and 2010 by Severity

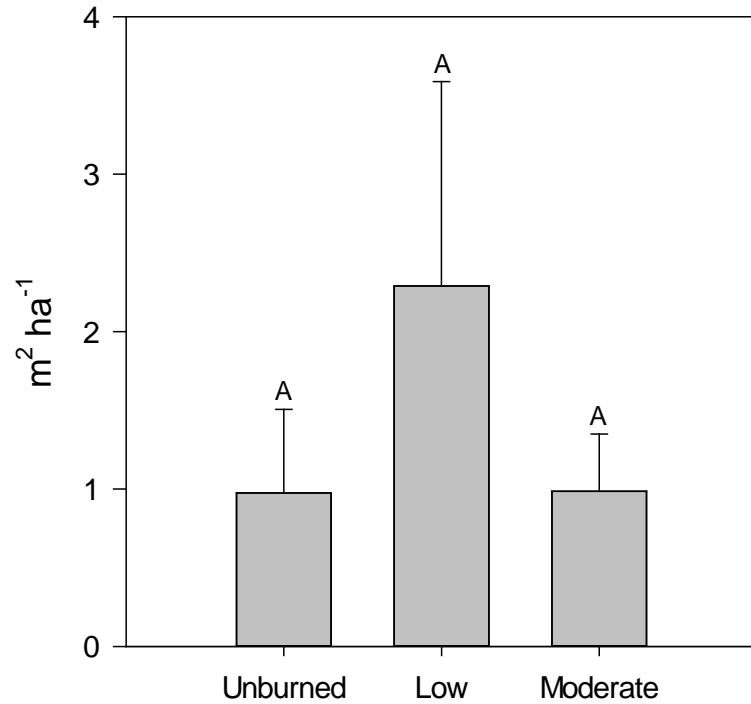


Figure 3. Mortality in unburned, low, and moderate severity sites was similar between 2005 and 2010. Basal area losses to mortality were not enough to substantially change stand structure or overall density.

Snags by Severity in 2010

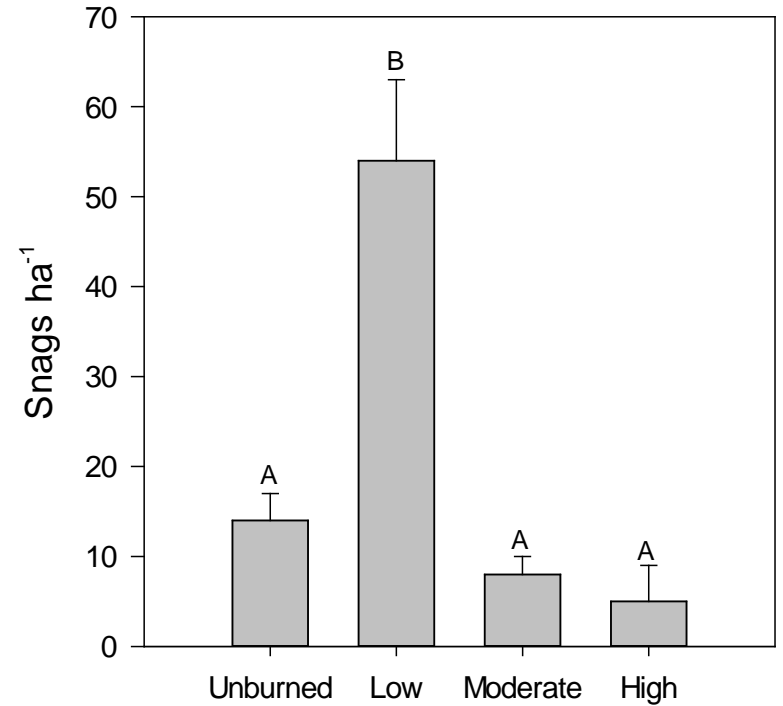


Figure 4. Low severity sites had significantly more standing snags per hectare than other burned and unburned severities. Future snag fall has the potential to influence forest floor biomass.

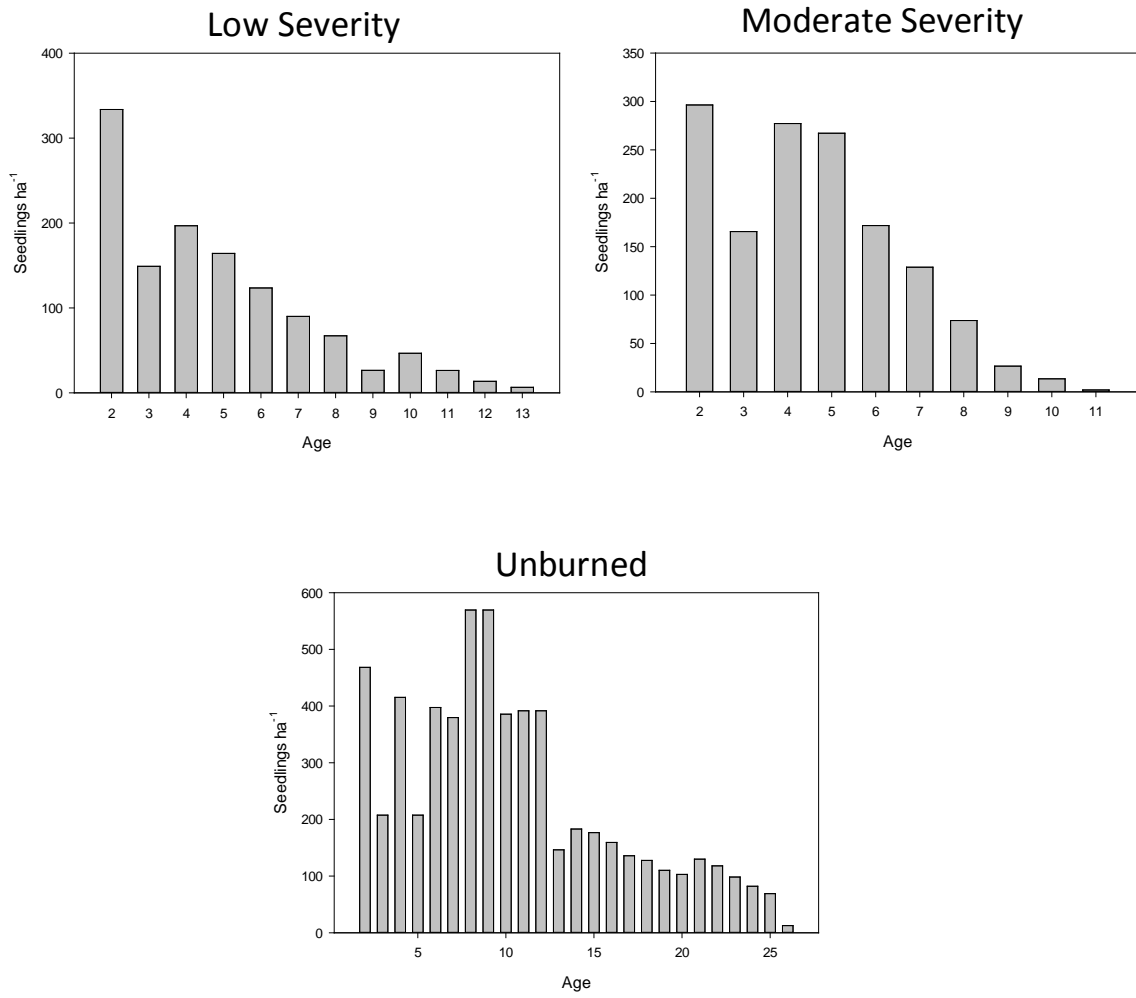


Figure 5. Seedlings ha⁻¹ by age show a lag in regeneration success immediately postfire with the most regeneration success beginning approximately 8 years postfire. More than 50 % of the seedlings in low and moderate severity sites established 7-9 years postfire.

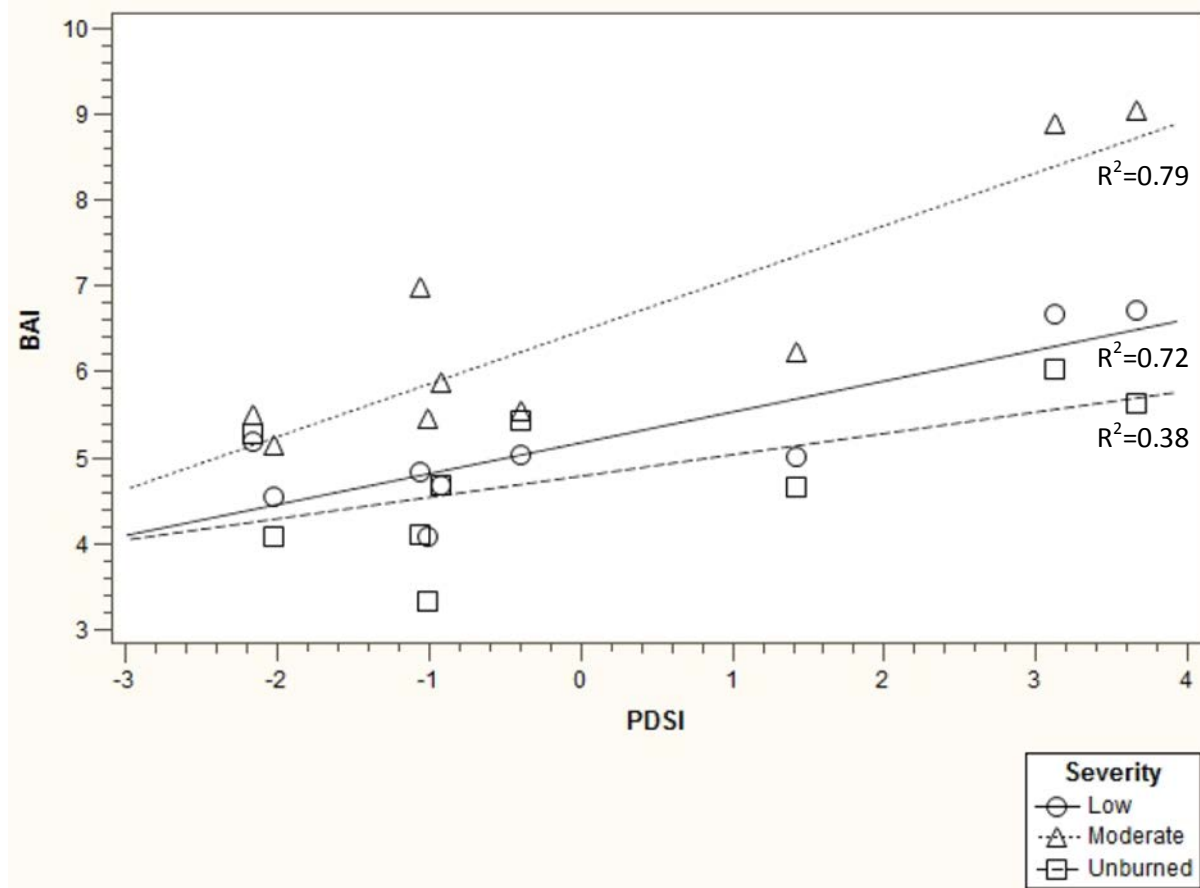


Figure 6. Postfire environmental conditions accounted for more variation in growth response than any fire effects and BAI increases with PDSI in unburned, low, and moderate severity areas in the 10 years following the Jasper Fire. Growth response was greatest in moderate severity sites. Each symbol represents the BAI for the 50 largest diameter trees in each severity for each year postfire with the corresponding PDSI rating.

Relative BAI for Fifty Largest Diameter Trees per Severity

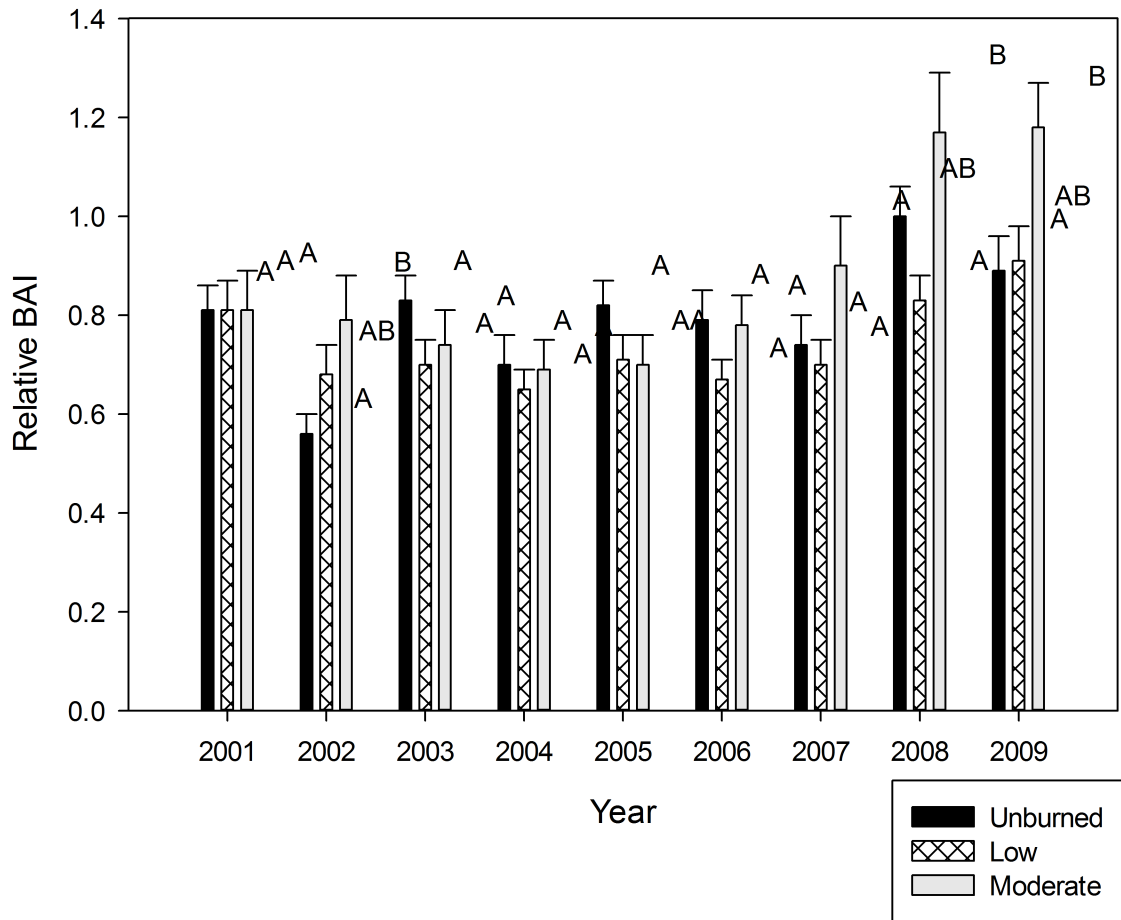


Figure 7. Relative basal area increment (BAI) indicated postfire radial growth was lower than the 5 year prefire average for unburned, low, and moderate severity sites until 2008. Growth in moderate severity sites was significantly higher in 2008 and 2009 and was the only severity to sustain postfire growth above prefire growth.

Change in Basal Area by Year and Severity

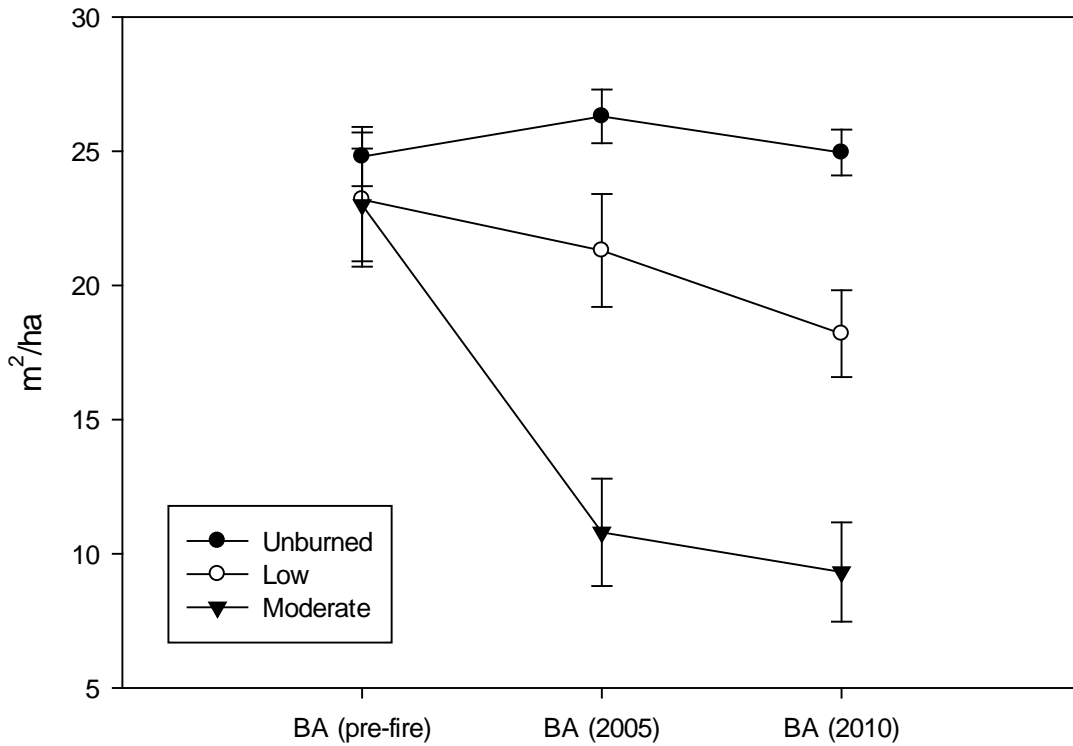


Figure 8. Basal area (BA) in moderate severity sites was decreased by more than 50 % in the five years following fire but was nearly the same loss (~1 m²) as unburned between 2005 and 2010. Low severity sites lost 8 % (~2 m²) of BA in the first five years and lost an additional 10 percent (2.3 m²) between 2005 and 2010.

Changes in Litter Layer by Year and Severity

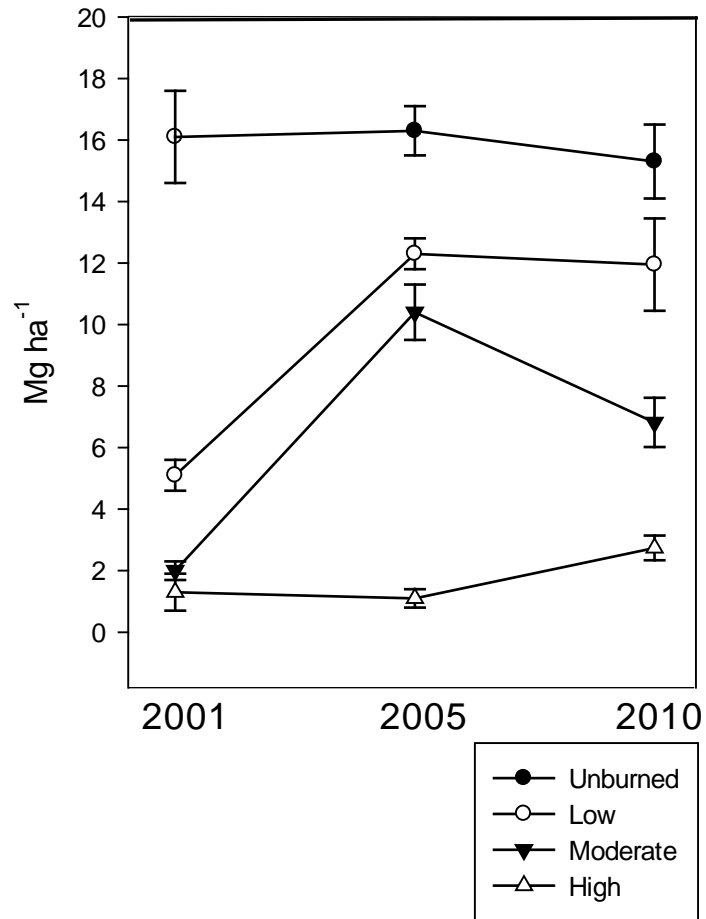


Figure 9. Litter accumulated quickly immediately following the fire as a result of needle cast. However, without a continued abundance of input material, litter amounts have not substantially accumulated between 2005 and 2010 in any burn severity.

Changes in FWD by Year and Severity

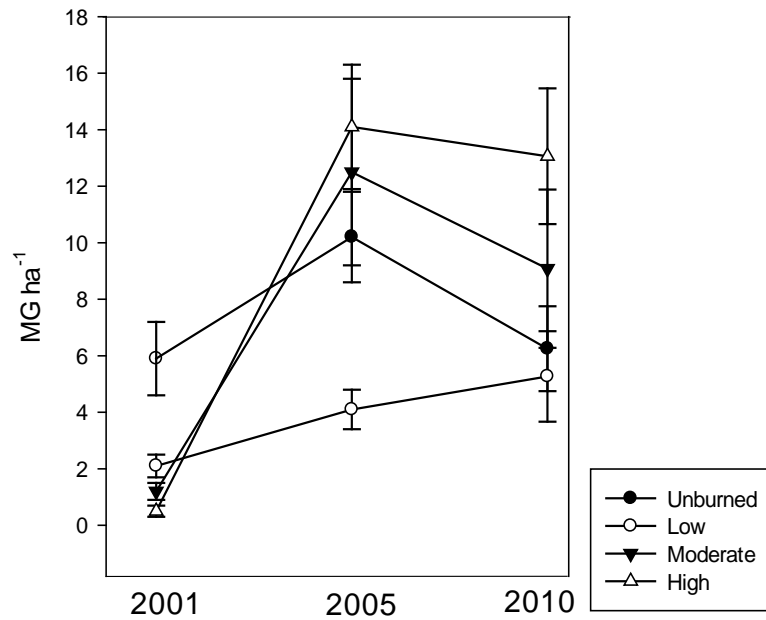


Figure 10. Fine woody debris (FWD) increased immediately following the fire in moderate and high severity sites while low severity sites remained below unburned areas. Changes in FWD between 2005 and 2010 have resulted in few significant differences within fuel size classes and fuels reductions from the fire have been negated in all burn severities.

Changes in CWD by Year and Severity

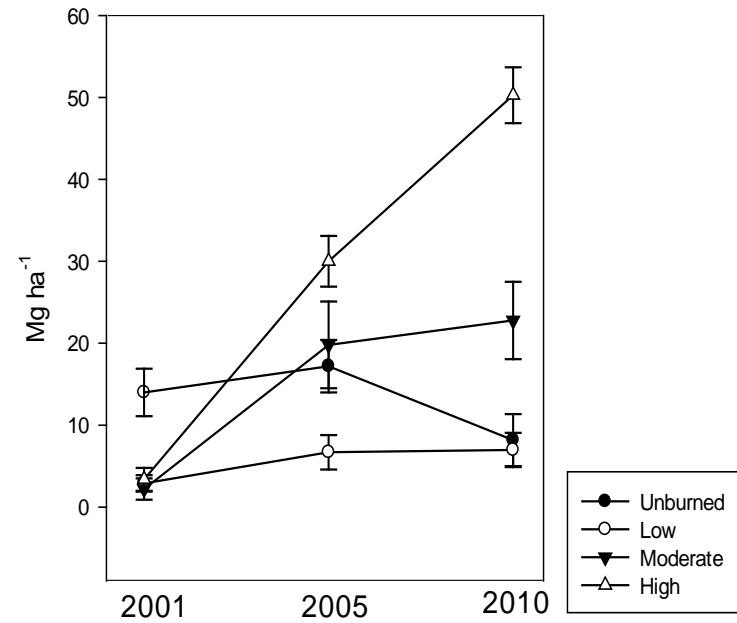


Figure 11. Initial reductions of coarse woody debris have been overcome by additions in all burn severities. High severity sites have accumulated ~50 Mg ha⁻¹ and account for ~80 % of total downed woody debris in those sites. Moderate and high severity sites are not likely to increase significantly above the 2010 amounts. Low and moderate severity sites were not significantly different from unburned sites 10 years postfire.

Changes in Duff Layer by Year and Severity

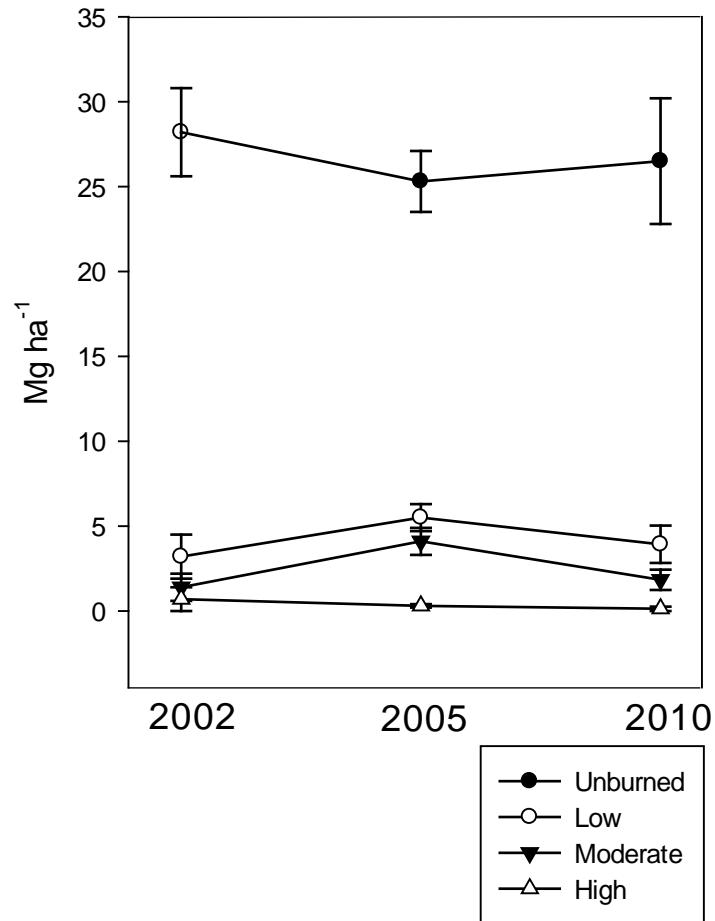


Figure 12. Duff has been slow to accumulate in all burn severities. Time needed for recovery of the duff layer will likely be measured by decades in areas that burned in the Jasper Fire.

PDSI Values by Year Pre and Post-fire

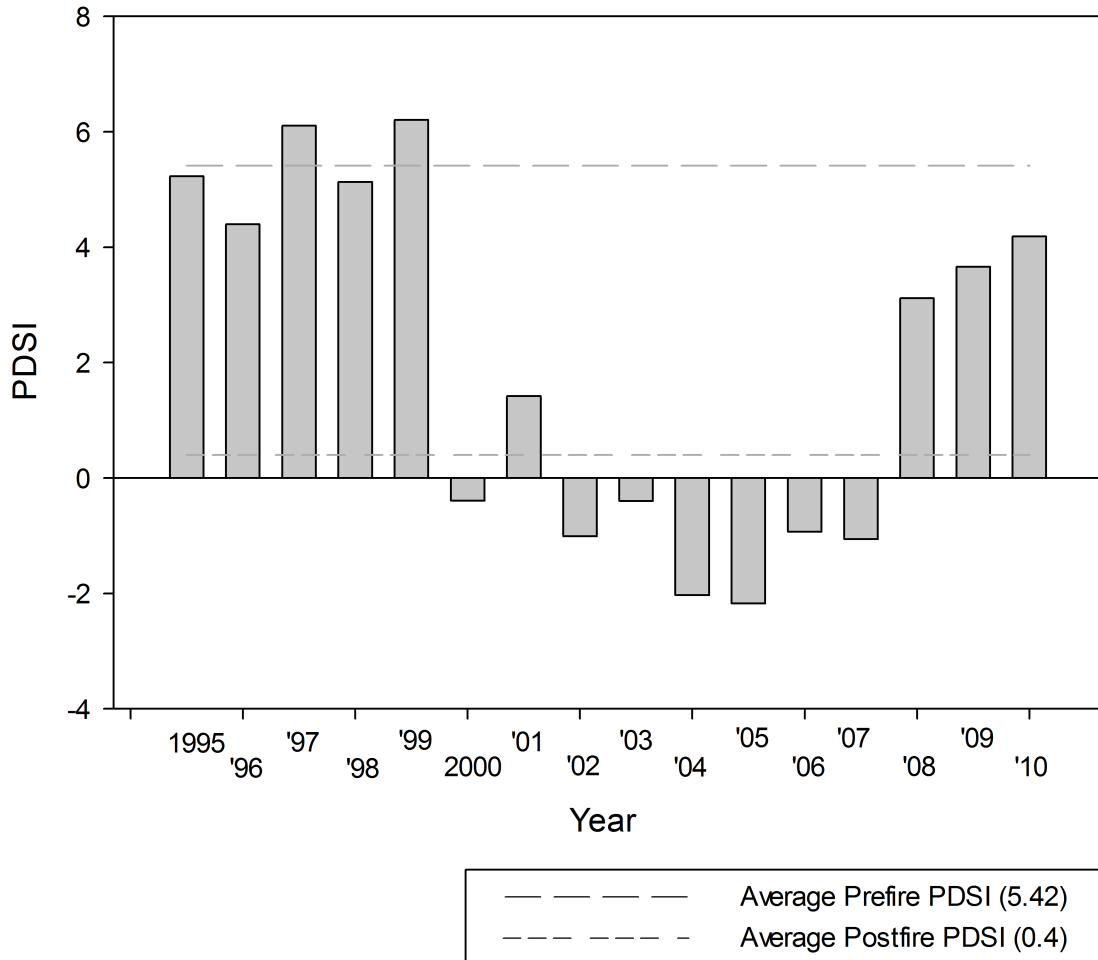


Figure 13. Palmer Drought Severity Index (PDSI) values five years prefire and ten years postfire for the Black Hills, South Dakota. Stated values are averaged over the months of June, July, and August. Values above zero indicate cool and moist conditions and values below zero indicate hot and dry conditions.

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