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Heterogeneity in fire severity within early season and late season prescribed burns in a mixed-conifer forest*

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Abstract. Structural heterogeneity in forests of the Sierra Nevada was historically produced through variation in fire regimes and local environmental factors. The amount of heterogeneity that prescription burning can achieve might now be more limited owing to high fuel loads and increased fuel continuity. Topography, woody fuel loading, and vegetative composition were quantified in plots within replicated early and late season burn units. Two indices of fire severity were evaluated in the same plots after the burns. Scorch height ranged from 2.8 to 25.4 m in early season plots and 3.1 to 38.5 m in late season plots, whereas percentage of ground surface burned ranged from 24 to 96% in early season plots and from 47 to 100% in late season plots. Scorch height was greatest in areas with steeper slopes, higher basal area of live trees, high percentage of basal area composed of pine, and more small woody fuel. Percentage of area burned was greatest in areas with less bare ground and rock cover (more fuel continuity), steeper slopes, and units burned in the fall (lower fuel moisture). Thus topographic and biotic factors still contribute to the abundant heterogeneity in fire severity with prescribed burning, even under the current high fuel loading conditions. Burning areas with high fuel loads in early season when fuels are moister may lead to patterns of heterogeneity in fire effects that more closely approximate the expected patchiness of historical fires.

Additional keywords: fire ecology; landscape heterogeneity; prescribed fire; season of burning.

Introduction

Prior to European settlement and modern-day fire exclusion, vegetation in the mixed-conifer zone of the Sierra Nevada was likely a complex mosaic of early and late successional stages, ranging from montane chaparral to old-growth forest (Bonnicksen and Stone 1982; Chang 1996; Russell *et al.* 1998; Nagle and Taylor 2005). Patch size was typically very small, ranging from a fraction of a hectare to several hectares (Franklin and Fites-Kaufmann 1996). This within-stand heterogeneity is believed to have been produced by and maintained through spatial and temporal variation in fire regime (including severity, frequency, and size), as well as local environmental and topographic variability (Kilgore 1973; Agee 1993; Chang 1996; Skinner and Chang 1996; Taylor and Skinner 1998; Beaty and Taylor 2001).

Spatial heterogeneity is a vital component of forests, promoting a greater diversity of flora (Martin and Sapsis 1992; Halpern and Spies 1995) and fauna (Chang 1996). Gaps within the forest canopy allow shade-intolerant species such as ponderosa pine (*Pinus ponderosa* Laws.) and giant sequoia (*Sequoiadendron giganteum* [Lindley] Bucholtz) to become established (Harvey *et al.* 1980). Survival and rate of growth of newly germinating tree seedlings is often especially pronounced in areas that burn with the greatest intensity (Harvey and Shellhammer 1991; Stephenson *et al.* 1991; Stephenson 1994). However, fires cannot be uniformly intense over large spatial scales, or the ability of the forest to regenerate would be reduced. The matrix of mature forest surrounding gaps is vital for recruitment, because the majority of seeds are typically dispersed in relatively close proximity to the parent trees (Nathan *et al.* 2000). Once seedlings become established, growing in gaps may allow these young trees to escape mortality from subsequent fires. Deposition of litter and woody surface fuels is reduced in gaps due to lack of an overstory fuel source. By the time trees are large enough to produce enough ground fuel to carry fire, they are also more likely to be large enough to survive fire (Cooper 1960, 1961; Kilgore 1973; Keeley and Stephenson 2000).

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Dramatic changes to forest structure and pattern have occurred in the Sierra Nevada mixed-conifer forest as a result of reduced fire frequency. In areas without a history of logging, the amount of forested area occupied by younger, early successional patches has declined and the amount of forested area occupied by dense intermediate-aged patches has increased (Bonnicksen and Stone 1982). Shade-tolerant tree species such as firs (*Abies* sp.) and incense cedar (*Calocedrus decurrens* [Torrey] Florin) have become more abundant at the expense of shade-intolerant species such as ponderosa pine and black oak (*Quercus kelloggii* Newb.), and the overall tree density is higher (Kilgore 1973; Vankat and Major 1978; Parsons and DeBenedetti 1979; Ansley and Battles 1998). In the absence of fire, forests may have become more structurally homogeneous (Bonnicksen and Stone 1980; Skinner 1995; Chappell and Agee 1996; Taylor 2000).

Another impact of the reduction in fire frequency in the mixed-conifer zone of the Sierra Nevada has been a substantial accumulation of surface fuels (Biswell *et al.* 1968; van Wagtendonk 1985) and greater fuel continuity (Miller and Urban 2000), both of which can increase the probability of large, high-intensity wildfires (van Wagtendonk 1985; Stephens 1998). Historically, frequent fires are believed to have resulted in low fuel loads and a patchy pattern of fire spread (Swetnam 1993). These fires burned predominantly at low-to-moderate intensity with patchy high intensity (Kilgore 1973; Stephenson *et al.* 1991; Stephenson 1999). Most overstory canopy trees survived in areas with lower-intensity fire, but groups of canopy trees were killed locally within a matrix of surviving trees in the higher-intensity areas (Stephenson 1999). This variability in fire behavior helped to maintain a patchy mosaic of vegetation and fuels. The size of high-severity patches produced when fire is reintroduced to the landscape may now be greater than it was historically (Keeley and Stephenson 2000).

The best means of reducing fuels and restoring a forest structure similar to the historical conditions is a source of debate (Bonnicksen and Stone 1985; Parsons *et al.* 1986; Stephenson 1999; Weatherspoon 2000). Bonnicksen and Stone (1985) have argued that prescription burning under the current fuel conditions could result in a more uniformly intense fire that is less likely to restore the desired landscape mosaic. This argument assumes that fuel loading and fuel continuity are the primary drivers of variability in fire severity in these forests and that both have become more homogeneous with fire exclusion. If other factors such as vegetation pattern, weather, topography, and ignition pattern also play an important role in generating variability in fire effects, prescribed fire alone may produce considerable forest heterogeneity, even under the current fuel conditions. Our understanding of patterns of landscape heterogeneity produced by prescribed fire and how this heterogeneity is affected by season of burning remains incomplete.

In the pre-Euro American Sierra Nevada, much of the area that burned did so during the dry late summer to early fall period (Caprio and Swetnam 1995). Most prescribed burning in Sequoia and Kings Canyon National Parks has, up to now, been done during the latter part of this same time period. However, because of poor air quality in the adjacent Central Valley, burning opportunities at this time of year are increasingly limited. As a result, only a fraction of the area necessary to maintain historical fire return intervals typically gets burned. Atmospheric conditions conducive to smoke dispersal are often more common during the spring to early summer period and expanding the burn window to include prescribed fire at this time of year allows more of the landscape to be treated.

Fuel moisture levels are typically higher in the spring and early summer than later in the season, which can strongly influence fire behavior and effects. Both the amount of heat generated and spread of fires is reduced at higher fuel moisture levels, owing to the energy required to vaporize water (DeBano *et al.* 1998; Nelson 2001). Computer models have shown fuel connectivity to be less at high fuel moisture levels (Miller and Urban 2000), and the depth of the forest floor fuel layer must be greater in order for combustion to propagate in moist duff (Miyanishi and Johnson 2002). Thus, early season burns in these mixed-conifer forests often consume less of the available fuel (Kauffman and Martin 1989; Knapp *et al.* 2005) and produce a patchier and less complete burn pattern (Knapp *et al.* 2005).

The purpose of the present study was to describe within-stand heterogeneity in fire severity resulting from early season and late season prescribed fire treatments, and to identify the relative importance of different topographic and biotic variables associated with this heterogeneity. Two components of fire severity were investigated: (1) scorch height; and (2) the percentage of the burnable ground surface that did burn.

Materials and methods

Study site description

Three early and three late season prescribed burn units were established, along with three control units, in an old-growth mixed-conifer forest within the watershed of the Marble Fork of the Kaweah River in Sequoia National Park. Each unit was 15–20 ha in size with irregular boundaries established along topographic features in accordance with National Park Service fire management concerns. The three control units were installed as part of another study and only the six burn units were used for the research reported in this paper. A map of the burn and control units is shown in Knapp *et al.* (2005).

Elevation in the study area ranged from 1900 to 2150 m above sea level and aspect was generally NW, although there was substantial micro-topographic variation. Tree species, in order of abundance, were white fir (*Abies concolor* [Gordon & Glend.] Lindley), sugar pine (*Pinus lambertiana*

Douglas), incense cedar, Shasta red fir (*A. magnifica* var. *shastensis* Lemmon), Jeffrey pine (*P. jeffreyi* Grev. & Balf.), ponderosa pine, mountain dogwood (*Cornus nuttallii* Audubon), and California black oak. The historical fire return interval in the study area was 27.4 years, but much of the study area had not burned since 1879 (A. C. Caprio and E. E. Knapp, unpublished data).

Pretreatment data collection

Ten 50 × 20 m (0.1 ha) plots were established within each of the six burn units (two treatments [early and late season burns] × three replicates [units] × 10 plots/unit = 60 plots total), in reference to a system of 36 permanent points on a 50-m grid. Plots were assigned randomly to 10 grid points and the direction of the plot was also random (one of four cardinal directions [0°, 90°, 180°, 270°]). Within each plot, diameter at breast height (dbh) was measured for all trees (dbh > 10 cm), and species and status (alive or dead) noted. Cover of herbaceous species, bare ground, and rock within the 0.1-ha plots was estimated by averaging the visual scores for twenty 1 × 1 m subplots systematically located within each plot. Cover was scored on the following scale: 1 = 0–1%; 2 = 2–10%; 3 = 11–25%; 4 = 26–50%; 5 = 51–75%; 6 = 76–100%. Cover scores were later converted back to a percentage, using the mean of each cover class range. Total herbaceous species cover was the sum of the cover of individual species.

Loading of woody fuels was estimated retrospectively using digital photographs taken of each plot from the midpoint of each 20-m side prior to the prescribed burns. Both small woody fuels (roughly including 1 h [<0.6 cm diameter], 10 h [0.6–2.54 cm diameter], and 100 h fuels [2.54–7.6 cm diameter]) and large woody fuels (1000 h [>7.6 cm diameter]) were visually scored (scale = 1–5, with 5 being the greatest amount of fuel) in all plots by seven different observers, and scores averaged. For an approximation of the actual fuel mass, the lowest small woody fuel score was similar to photo 1-PP-4 in a photo series depicting fuel loadings with different tree composition and size classes in the northern Sierra Nevada and southern Cascades (Blonski and Schramel 1981), whereas the highest small woody fuel score was similar to photo 2-MF-4. The large woody fuel scores approximated fuel mass values associated with photos 1-MF-4 to 5-MF-4 in the same photo series. Loading of litter and duff fuels could not be estimated from photographs, but both should be highly correlated with the basal area of trees within the plot.

Slope and aspect of each plot were calculated by overlaying the spatial coordinates of the nearest gridpoints with a 10-m-resolution digital elevation model in a geographic information system (GIS). Slope and aspect enabled an index of the potential total yearly heat load for each plot to be estimated, using equation 3 of McCune and Keon (2002). Potential total yearly heat load is proportional to the amount of direct incident solar radiation intercepted by a given aspect and slope, corrected for the fact that aspects with afternoon sun will have higher maximum temperatures than aspects with morning sun. Heating as a result of solar radiation will influence the amount of moisture contained within fuels (Byram and Jemison 1943), and variability in the potential heat load within the burn units may therefore be predictive of variability in fuel moisture at the same scale.

Prescribed burns

Early season burns were conducted on 20 and 27 June 2002, and late season burns were conducted on 28 September, 17 October, and 28 October 2001. Whereas the early season burns occurred approximately 6 weeks following the end of snow melt, the late season burns were preceded by over 4 months of mainly dry summer and early fall weather. Weather conditions and fuel moisture levels were very similar for burns within the same burning season treatment. One estimate of fuel moisture was made per unit immediately prior to ignition. Fuels were sampled widely outside of the plots in order to limit influence on fire behavior and effects resulting from disturbance of the fuel bed within the plots. Fuel moisture was significantly higher for the early season than the late season burns (Knapp *et al.* 2005). Average temperature, relative humidity, and maximum wind speed during the ignition period were 20°C, 52%, and 3 km h^{-1}, respectively, for the early season burns, and 15°C, 44%, and 3 km h^{-1}, respectively, for the late season burns. Using drip torches, strip head fires spaced ~10–15 m apart were ignited progressively from higher to lower elevations. With the exception of occasional single small trees that torched, fire was predominantly on the surface. Flame lengths were generally less than 1 m, except in areas with an abundance of large downed logs.

Post-treatment data collection

Scorch height, defined as the maximum height of complete needle kill, was measured on all trees within plots 2–9 months post burn, using a laser rangefinder. Scorch height often varied on different sides of a tree and was therefore measured at both the point of maximum height above ground and on the side of the tree opposite of where the maximum scorch height occurred. The two values were then averaged. Scorch height was not determined for trees that were completely scorched or trees with a base of live crown located above the scorching level. Percentage of the ground surface containing fuel that burned (hereafter referred to as ‘percentage of area burned’ for ease of explanation) was quantified for each plot as the average of visual scores within twenty 1 × 1 m subplots systematically located in each plot, to the nearest 10%. We felt that this was more accurate than making one visual estimate of percentage of area burned for the entire plot, because whether or not an area burned could often be determined only by close observation. Rocks were not considered in the visual estimates and the percentage of bare ground prior to the burns was subtracted from the field values; the percentage of area burned variable was therefore the percentage of the area burned that contained fuel and potentially could have burned.

Percentage of area burned was evaluated during the first full growing season following completion of the prescribed burn in that unit. This was the earliest time at which the late season units could be entered owing to snow cover (snow began falling within days after completion of the burns). The early season burn units were evaluated the same way for consistency. More measurement error is likely associated with the early season than the late season percentage area burned estimates, owing to a heavy rainstorm in November 2002, which caused some soil erosion and made the boundaries between burned and unburned patches more difficult to distinguish.

Data analysis

Frequency histograms for scorch height and percentage of area burned were constructed to demonstrate the variation among plots in these two variables. Significance of differences between treatments was determined with one-way analyses of variance. Levene's test was performed on the residuals to determine if differences in the amount of among-plot variability existed. The Kolmogorov–Smirnoff goodness-of-fit test was used to evaluate the significance of differences in frequency histograms between treatments.

Mixed model analyses of variance (PROC MIXED; SAS Institute, Cary, NC, USA) were used to investigate factors most closely associated with scorch height and percentage of area burned. Slope, potential annual heat load, small woody fuel score, large woody fuel score, tree basal area, percentage of tree basal area composed of pine, herbaceous species cover, and bare ground or rock cover were fixed effects, whereas burn unit was random.

Slope affects flame length and rate of spread. Other variables that influence fire behavior directly, such as fuel moisture, fuel loading, and fuel bulk density, are more difficult to obtain accurate estimates of at the plot scale, but differences in these variables may have been captured by variables that were easier to measure. For example, potential heat load may be predictive of fuel moisture, because fuel moisture is expected to be lowest on SW-facing aspects and slopes perpendicular to the sun angle, where heat load is the greatest. Basal area of trees does not influence fire behavior directly because live trees in this system typically do not act as fuel, but basal area may be correlated with among-plot differences in fuel moisture, owing to the influence of shading by the canopy. Basal area also indirectly influences how much litter, duff, and small woody fuel is potentially deposited on the forest floor – the greater the tree volume, the more litter, duff, and small woody fuel production is expected. The percentage of basal area composed of pine may be an indicator of litter flammability because the lower bulk density of pine litter causes it to burn more readily than fir and other short-needled litter (Agee *et al.* 1978; van Wagtendonk *et al.* 1998). In addition, lower bulk density litter dries faster to the point where combustion is possible (Stephens 2001). The herbaceous species cover variable was possibly a predictor of fine-scale soil and fuel moisture differences because the presence of understory vegetation was generally highest in moister microsites. Most abundant herb species included bracken fern (*Pteridium aquilinum* [L.] Kuhn var. *pubescens* L. Underw.), hawkweed *Hieracium albiflorum* Hook., and violet draperia (*Draperia systyla* [A. Gray] Torrey), which in total comprised 56% of the herbaceous cover (E. E. Knapp, D. W. Schwilk, J. M. Kane and J. E. Keeley, unpublished data). The amount of bare ground and rock was a predictor of how much area lacked fuel and potentially provided quantification of the degree of fuel continuity.

The scorch height variable approximated a normal distribution and did not require transformation. The percentage of area burned variable was arcsine square root transformed prior to analysis to improve normality.

Results

Scorch height

Scorch height did not differ between burn season treatments (early = 11.1 m; late = 13.5 m; $F = 1.41$, $P = 0.240$), but was highly variable among plots, ranging from 2.8 to 25.4 m in the early season burns, and from 3.1 to 38.5 m in the late season burns (Table 1, Fig. 1). Analysis of variance conducted on the absolute value of the residuals (Levene's test) indicated that the amount of variability in scorch height generated by the burns also did not differ between the burn season treatments ($P = 0.181$). In addition, the scorch height frequency distributions for the two seasons (Fig. 1) were very similar (Kolmogorov–Smirnov test, $P = 0.995$).

Factors associated with variation in scorch height

When analyzed together in a mixed-model ANOVA, the variables most strongly associated with scorch height were slope, tree basal area, percentage of basal area composed of pine, and small woody fuel score, in order of significance (Table 2). Scorch height was greatest in plots on steeper slopes, plots containing more tree basal area, plots with a higher percentage of pine relative to short-needled species such as fir and incense cedar, and plots with abundant small woody fuel. The burn season variable approached significance ($P = 0.134$).

The large number of main effects made it impossible to analyze all possible two-way interactions without sacrificing most of the statistical power of the model. Therefore analysis of interactions was conducted in an exploratory manner, including only the two-way interactions among the four significant ($P < 0.05$) main effects in a separate mixed-model ANOVA. Of these, only slope × percentage of basal area composed of pine was significant ($P = 0.043$). When the non-significant interactions were removed, and the model

Table 1. Means and ranges for independent and dependent variables measured within early season and late season burn treatment units

Variable	Early season burn		Late season burn	
	Average	Range	Average	Range
Slope (degrees)	16.5	9.0–29.5	18.7	10.6–31.8
Heat load index[A]	0.99	0.84–1.07	0.93	0.71–1.07
Small woody fuel score (scale = 1 to 5)	3.09	1.79–4.38	2.75	1.31–4.19
Large woody fuel score (scale = 1 to 5)	2.24	1.10–3.79	2.14	1.24–4.57
Basal area (m^2/ha)	69.5	25.6–117.9	67.8	31.3–115.2
Pine basal area (%)	26.0	0–73.1	25.7	0–80.2
Herbaceous cover (%)	7.7	0–24.4	17.4	1.6–51.8
Bare ground/rock cover (%)	6.7	0–43.9	5.1	0–21.9
Scorch height (m)	11.1	2.8–25.4	13.5	3.1–38.5
Plot area burned (%)	70	15–96	88	48–100

[A] Calculated using formula #3 of McCune and Keon (2002).

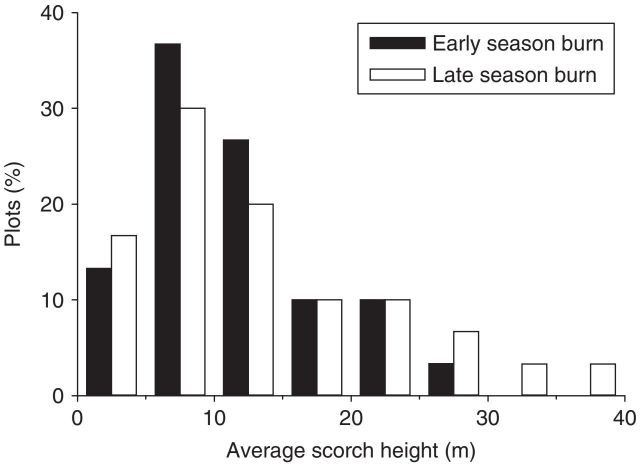

Fig. 1. Percentage of plots within different average scorch height (m) categories in both early season ($n = 30$) and late season ($n = 30$) prescribed burning treatments.

Table 2. Significance of fixed effects in a mixed-model analysis of variance of average scorch height for prescribed burns conducted in early and late season

The random effect (unit) was not significant ($P = 0.351$). Denominator degrees of freedom (d.d.f.) are based on Satterthwaite's approximation. n.d.f., numerator degrees of freedom

Fixed effect	n.d.f.	d.d.f.	*F*	*P*
Burn season	1	3.23	3.96	0.134
Slope	1	22	10.79	0.003
Head load	1	16.2	1.21	0.287
Small woody fuel score	1	48.5	4.82	0.033
Large woody fuel score	1	49	0.55	0.460
Basal area	1	46.8	7.82	0.008
Pine basal area (% of total)	1	47.8	7.16	0.010
Canopy closure	1	48.1	0.50	0.484
Herbaceous cover	1	20.4	0.28	0.606
Bare ground and rock cover	1	45.6	1.37	0.248

containing all main effects and the one significant interaction was run again, explanatory power, as expressed by Aikake's Information Criterion (AIC), was reduced relative to the model containing only the main effects. The mixed-model ANOVA including the slope × percentage of basal area composed of pine interaction is therefore not shown.

Percentage of area burned

The percentage of area burned varied substantially among plots, ranging from 15 to 96% in the early season burn units and from 47 to 100% in the late season burn units (Table 1, Fig. 2). Overall, significantly less area burned in the early season than in the late season (early season mean = 70%; late season mean = 88%; $F = 24.66$, $P < 0.001$). (The actual total plot area that burned was somewhat less because an average of 6% of the study area contained bare ground and rock prior to the burns, and this was factored out of the percentage of area burned estimates.) Variance in the percentage of area burned tended to be greater in the early season than the late season (Levine's test, $P = 0.080$). The difference in frequency distribution of percentage of area burned between seasons was strongly significant (Kolmogorov–Smirnov test, $P < 0.001$) (Fig. 2).

Factors associated with variation in percentage of area burned

When analyzed together in a mixed-model ANOVA, the variables most strongly associated with percentage of area burned were cover of bare ground and rock, burn season, and slope, in order of significance (Table 3). Percentage of area burned was greatest in plots containing less bare ground and rock, in plots burned in the fall, and in plots on steeper slopes. Percentage of basal area composed of pine and small woody fuel score approached significance ($P = 0.118$, $P = 0.097$, respectively), with a tendency for greater percentage of area burning in plots with a higher percentage of pine and in plots where loading of small woody fuels was high.

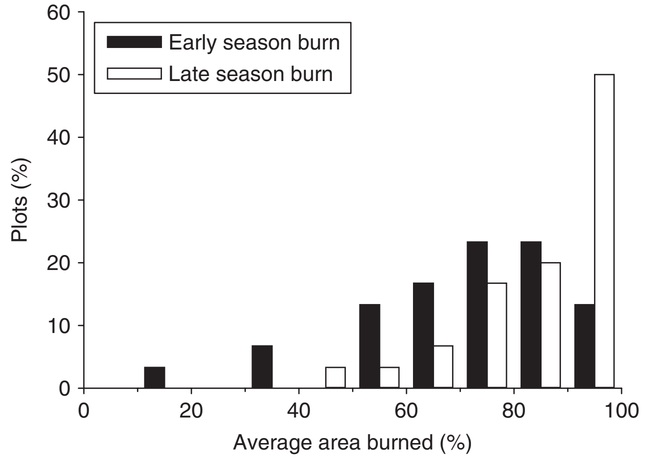

Fig. 2. Percentage of plots within different average percentage of area burned categories in both early season ($n = 30$) and late season ($n = 30$) prescribed burning treatments.

Table 3. Significance of fixed effects in a mixed-model analysis of variance of percentage of area burned for prescribed burns conducted in early and late season

The random effect (unit) was not significant ($P = 0.496$). Percentage of ground surface area burned was arcsine square root transformed prior to analysis. Denominator degrees of freedom are based on Satterthwaite's approximation

Fixed effect	n.d.f.	d.d.f.	*F*	*P*
Burn season	1	3.57	18.97	0.016
Slope	1	13.4	5.50	0.035
Head load	1	11.3	0.88	0.368
Small woody fuel score	1	49	2.66	0.110
Large woody fuel score	1	48.6	0.35	0.554
Basal area	1	47.6	0.12	0.735
Pine basal area (% of total)	1	48.6	2.38	0.129
Canopy closure	1	45.9	0.00	0.945
Herbaceous cover	1	17.3	0.01	0.924
Bare ground and rock cover	1	39.6	8.54	0.006

A separate exploratory mixed-model ANOVA was run to investigate possible two-way interactions among the three significant ($P < 0.05$) main effects. None of these interactions were found to be significant or add to the explanatory power of the model as expressed by AIC. The final model presented in Table 3 therefore includes only the main effects.

Discussion

The abundance of fuels that have accumulated in many forested areas has led to a concern that fire effects generated by prescription burning might now overwhelm mechanisms that historically generated heterogeneity in fire severity, leading to greater than desired landscape uniformity. Our results illustrate that substantial variation in two measures of fire severity – scorch height and percentage of area burned – can be produced by both early season and late season prescribed burns, even after over a century of fire suppression. Whereas several of the independent variables significant in the ANOVAs of scorch height were direct or indirect measures of fuel loading (small woody fuel score, tree basal area), other topographic and biotic factors also likely contributed to this heterogeneity. The importance of slope, the independent variable with the strongest significance, was expected because rate of fire spread increases with slope steepness (Agee 1993), and fireline intensity is higher when more fuel is consumed per unit time. In addition, hot air is more readily convectively lifted into tree crowns on slopes, contributing to greater scorching. Percentage basal area composed of pine was also important in explaining variation in scorch height, likely because fire in pine litter produces greater flame lengths than fire in the more compact litter of shorter-needled conifer species (Fonda *et al.* 1998). This relationship between proportional abundance of pines and height of crown scorching has been noted with wildfire as well (Weatherspoon and Skinner 1995).

Most of the independent variables significant in the ANOVA of percentage of area burned were more strongly related, either directly or indirectly, to fuel continuity rather than fuel loading. Less of the burnable area was burned in plots containing more bare ground and rock, presumably because these barriers can limit fire spread. Significance of burn season was likely largely the result of greater fuel moisture in the early season. Effective fuel continuity is less at higher fuel moisture levels (Miller and Urban 2000) because the likelihood that adjacent fuel particles will become heated to the point of combustion is reduced (Nelson 2001), limiting fire spread. Our finding of greater burn patchiness with prescribed fires conducted under higher fuel moisture conditions is consistent with other studies (e.g. Slocum *et al.* 2003).

The third significant independent variable, slope, was positively associated with the amount of area burned, presumably because fuels are exposed to greater convective and radiant heat on slopes, making preheating more effective (Rothermel 1972). The variables 'amount of small woody fuel' and 'percentage basal area composed of pine' both approached statistical significance and may have also influenced the percentage of area burned. Fuel continuity was expected to be greater in areas with more fine fuels and a higher proportion of long-needled conifers such as pine. Fire carries more readily in pine litter than in the litter of shorter-needled species, owing to lower bulk density of the pine litter (Agee *et al.* 1978; van Wagtendonk *et al.* 1998; Stephens *et al.* 2004). Miller and Urban (2000) reported that bulk density, in addition to fuel moisture, played a role in controlling area burned in fire spread models. High bulk density litter of short-needled conifer species dries more slowly to the point where combustion is possible after snows melt, potentially resulting in a shorter burning season (Stephens 2001). Agee *et al.* (1978) noted that pine fuels could be effectively reduced by burning in the spring, summer, or fall, but white fir and other short-needled fuels required drier conditions in the summer and fall.

Other factors besides those included in the ANOVA models, such as weather and how fire was applied during the prescription burn, also likely contributed to the observed heterogeneity in fire severity. The number of igniters applying fire at one time, the horizontal distance between igniters, and the time between passes were variable and all can strongly influence fire severity. In addition, some breaks in ignition occurred when fire crews were preoccupied with burning snags or spot fires. Plots that burned during these times may have experienced reduced fire intensity (more backing fire, less heading fire). It was not possible to quantify these ignition factors at the plot scale, owing to operational constraints. Because weather conditions were mild and relatively consistent during all of the burns, variation in fire severity was probably less strongly influenced by weather than by ignition patterns. Still, variability in relative humidity and wind speed were likely sufficient to exert some influence on fire behavior. Although weather variables were recorded hourly during the burns, they were not included in the ANOVA models because it was difficult to determine exactly when each plot burned and to match weather conditions at that time. Another factor we did not quantify – proximity to water courses – has been shown to exert a strong influence on fire effects, presumably because of species composition and fuel moisture differences (Russell and McBride 2001; Skinner 2003). However, most water courses within the units in the present study were ephemeral and did not contain water at the time of the burns.

It is not known how the relative contribution of fuel loading-related and non-fuel loading-related factors for generating variation in fire severity compared to historical fires, but the role of non-fuel loading variables in generating heterogeneity under current conditions is perhaps under appreciated. The strong positive association between percentage of basal area composed of pine and scorch height (and to a lesser extent, percentage of area burned) suggests that some of the capacity of prescribed fires to generate a heterogeneous post-burn landscape might be jeopardized in the future by shifts in species composition away from pine. Whereas shade-tolerant species with less flammable and more compact litter have always been part of the mixed-conifer forest, they have become more abundant as a result of fire suppression and shade-intolerant species with more flammable litter, such as ponderosa pine and Jeffrey pine, have become less abundant. In addition, sugar pine is in decline, due in part to white pine blister rust, and may play a lesser role in forests of the future (van Mantgem *et al.* 2004). Loss of pines may be reducing the extent of the historical mosaic of long-needled and short-needled species.

Forest gap models parameterized with data from the Sierra Nevada predict that surface fire regimes should increase the fine-scale spatial heterogeneity in some components of forest structure, over that found in the absence of fire (Miller and Urban 1999). Of interest to resource managers is whether the heterogeneity produced by prescribed burns is comparable to the heterogeneity that was produced historically by natural fires. To modulate fire behavior and aid in control, prescribed fires are often ignited in strips and also conducted within a relatively narrow range of weather and fuel moisture conditions compared with historical fires. All potentially reduce heterogeneity in the burning pattern. However, the weather and fuel conditions under which prescribed fires are conducted may also be what maximize heterogeneity in burn patterns produced by other mechanisms. Model outputs of Miller and Urban (2000) indicate that connectivity of fuels influences fire spread under moderate weather conditions, but that this relationship diminishes under dry and windy conditions. Dry, windy conditions can lead to intense fire and uniform fire coverage over large areas, despite heterogeneity in the arrangement of fuels. In addition, fuel connectivity is a function of fuel moisture mainly at intermediate fuel moisture levels (Miller and Urban 2000). Model outputs of Miller and Urban (2000) predict that at low fuel moisture levels, much of the area will burn regardless of patterns of fuel connectivity. At high fuel moisture levels, little of the area burns. Both of the latter situations limit the amount of heterogeneity potentially produced by fire. Thus the heterogeneity in fire severity that results from conducting prescribed burns within a relatively narrow window of weather and fuel moisture conditions may to some extent compensate for the heterogeneity historically generated by variability in weather that natural fires burned under.

Heterogeneity in fire severity may play an important ecological role. Unburned or less severely burned patches provide refugia for plant and animal species and propagules for recolonizing more severely burned areas. Such patchiness can also slow erosion and increase infiltration of run-off (Martin and Sapsis 1992). Whereas both early and late season prescribed burns in the present study produced abundant heterogeneity in fire severity, patchiness in the percentage of area burned in the early season may be more similar to the patchiness of historical fires that typically burned under lower fuel moisture conditions but when fuel loading was not as high, or fuels as continuous. Even with the abundance of fuel in many forested areas today, variability in other factors may still be sufficient for prescribed fires conducted under moderate weather and fuel moisture conditions to produce a highly heterogeneous post-burn landscape.

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