Effects of prescribed fire and season of burn on direct and indirect levels of tree mortality in Ponderosa and Jeffrey Pine Forests in California, USA

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A B S T R A C T

Many forests that historically experienced frequent low-intensity wildfires have undergone extensive alterations during the past century. Prescribed fire is now commonly used to restore these fire-adapted forest ecosystems. In this study, we examined the influence of prescribed burn season on levels of tree mortality attributed to prescribed fire effects (direct mortality) and bark beetles (Coleoptera: Curculionidae, Scolytinae) (indirect mortality) in ponderosa pine, Pinus ponderosa Dougl. ex Laws., and Jeffrey pine, Pinus jeffreyi Grev. and Balf., forests in California, USA. A total of 816 trees (9.9% of all trees) died during this 3-yr study. Significantly higher levels of tree mortality (all sources) occurred following early and late season burns compared to the untreated control, but no significant difference was observed between burn treatments. The majority (461 trees) of tree deaths were attributed to direct mortality from prescribed burns and was strongly concentrated (391 trees) in the smallest diameter class (<20.2 cm diameter at breast height, dbh). For the largest trees (>50.7 cm dbh), significantly higher levels of tree mortality occurred on early season burns than the untreated control, most of which resulted from indirect mortality attributed to bark beetle attacks, specifically western pine beetle, Dendroctonus brevicomis LeConte, and mountain pine beetle, D. ponderosae Hopkins. Red turpentine beetle, D. valens LeConte, was the most common bark beetle species found colonizing trees, but tree mortality was not attributed to this species. A total of 355 trees (4.3% of all trees) were killed by bark beetles. Dendroctonus brevicomis (67 trees, 18.9%) and D. ponderosae (56 trees, 15.8%), were found colonizing P. ponderosa; and Jeffrey pine beetle, D. jeffreyi Hopkins, was found colonizing P. jeffreyi (seven trees, 2.0%). We also found pine engraver, Ips pini (Say) (137 trees, 38.6%), and, to a much lesser extent, Orthotomicus (=ips) latidens (LeConte) (85 trees, 23.9%) and emarginate ips, I. emarginatus (LeConte) (3 trees, 0.8%) colonizing P. ponderosa and P. jeffreyi. Few meaningful differences in levels of indirect tree mortality attributed to bark beetle attack were observed between early and late season burns. The incidence of root and root collar pathogens (Leptographium and Sporothrix spp.), including species known to be vectored by bark beetles, was low (18% of trees sampled). The implications of these and other results to management of P. ponderosa and P. jeffreyi forests are discussed in detail.

1. Introduction

Many fire-adapted forest ecosystems in the western USA are denser and more spatially homogenous, have more small trees and fewer large trees, and have much higher fuel loads than prior to Euro-American settlement. Such conditions are prevalent nationally, but most notable at lower elevations in the western USA where short-interval, low-moderate intensity fire regimes pre-

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of small-diameter trees and fire-intolerant tree species by low-intensity surface fires, and competitive exclusion of tree seedlings by understory grasses, are believed to have maintained such conditions (Oliver, 2000).

In recent yr, large and severe wildfires have heightened public concern in the western USA. Currently, >10 million ha of forests are classified as having moderate to high fire hazards (Stephens and Ruth, 2005) and fuel reduction treatments have been widely promoted to reduce future wildfire impacts. Prescribed fire is now commonly used to reduce the buildup of hazardous fuels and to restore fire-adapted forest ecosystems (Agee and Skinner, 2005). Generally, prescribed burns are effective at reducing fire hazard (Pollet and Omi, 2002) particularly when canopy bulk density is low enough so that active crown fire spread is unlikely (Fulé et al., 2002; Agee and Skinner, 2005), as is typical of some P. ponderosa and P. jeffreyi forests. Mechanical fuel treatments (e.g., thinning from below) are also used, but have functionally different effects from prescribed burns on the fuel matrix and load within each fuel component.

In the Sierra Nevada of California, USA, high surface fuel moistures occur during late spring after snow melt or following the first rains or snow in mid- to late fall (Fig. 1). Historically, wildfires occurred most frequently in the late summer and early fall (van Wagendonk, 1972; Kilgore, 1973) during periods of peak lightning ignitions and lowest fuel moistures. Accordingly, late season (fall) prescribed burns are thought to more closely mimic natural patterns and processes, and therefore have often been favored by forest managers. The onset of fall precipitation also reduces the chance of fire escapes. However, late season burns coincide with stable atmospheric conditions when smoke dispersal is poor, and when forest managers face substantial restrictions on when burns may be implemented due to air quality concerns (Cahill et al., 1996). Furthermore, in fall it is possible to go directly from conditions too hot and dry to conduct prescribed burns to substantial snow cover, which effectively eliminates the fall burn window.

In order to meet their burn goals (e.g., acreage targets), forest managers are increasingly conducting burns during the early season (spring) when atmospheric conditions may be more favorable. Early-season burns generally allow for conducting treatments when suitable fuel moistures are more consistent (i.e., little precipitation occurs during this time of yr in the Sierra Nevada), and are not reliant on recent or impending precipitation, as is the case in fall. However, forest managers are concerned about potential increases in the amount of tree mortality, both direct tree mortality attributed to prescribed fire effects and indirect tree mortality attributed to bark beetle (Coleoptera: Curculionidae, Scolytinae) attack, during and immediately following early season burns. Early season burns occur at the beginning of the annual growth period when plants are most susceptible to heat damage and when carbohydrate reserves are at their lowest levels (Hough, 1968). Furthermore, it has been reported that burns implemented during the growing season result in greater amounts of tree mortality than those implemented during the dormant season, and may also cause increased amounts of fine root damage (Swezy and Agee, 1991). On the other hand, late season burns are likely to be of greater intensity (Skinner and Chang, 1996), and have been reported to result in greater amounts of tree mortality than early season burns (Thies et al., 2005). Schwilk et al. (2006) reported levels of tree mortality were related to fire intensity rather than differences in tree phenology in Sequoia National Park, USA.

Levels of tree mortality following prescribed burns depend on numerous factors including, but not limited to, tree species, tree size, phenology (season or life history stage), degree of fire-caused injuries, initial and post-fire levels of tree vigor, the post-fire environment, and the frequency and severity of other predisposing, inciting and contributing factors (Knapp et al., 2009). Prescribed burns may influence the amount of bark beetle-caused tree mortality by affecting the vigor of residual trees; the size, distribution and abundance of preferred hosts; and the physical environment within forest stands (Parker et al., 2006; Fettig et al., 2007). Volatiles released from fire-injured trees include monoterpenes that are known to influence the physiology and behavior of tree-killing bark beetles (Seybold et al., 2006). Early season burns stress trees just prior to the major flight activity periods of many bark beetles (Fettig et al., 2004b, 2005). McGugh et al. (2003) examined the response of several bark beetle species to a spring wildfire, summer wildfire and fall prescribed fire in Arizona, USA. The percentage of trees attacked by Dendroctonus and Ips species was lowest following the fall burn (11% of total trees), intermediate following the summer wildfire (19%) and highest after the spring wildfire (41%). Schwilk et al. (2006) found the probability of bark beetle attack (several species) on pines did not differ between early and late season burns while the probability of attack on firs, Abies spp., was greater following early season burns.

The propensity for bark beetles to attack fire-injured trees has led to questions regarding how the amount and distribution of bark beetle-caused tree mortality affect efforts to restore fire-adapted forest ecosystems with prescribed fire (Parker et al., 2006). Concerns exist about the potential for bark beetle populations to increase in fire-injured trees and then colonize apparently healthy trees in adjacent areas (Rasmussen et al., 1996). Furthermore, little is known about the effects of prescribed fire on root and/or root collar fungal infections (e.g., from Leptographium spp.) that may be introduced by attacks from certain bark beetles, such as red turpentine beetle (RTB), D. valens LeConte. The primary objectives of this 3-yr study were to determine the effect of prescribed burn season on levels of tree mortality, levels of tree mortality attributed to prescribed fire effects (direct mortality), and levels of tree mortality attributed to bark beetle attack (indirect mortality) in P. ponderosa and P. jeffreyi forests. A secondary objective was to determine the incidence of root and root collar pathogens following the application of prescribed fire.

2. Materials and methods

2.1. Study site and associated conditions

This study was conducted on the Truckee Ranger District, Tahoe National Forest, California (39.45’ N, 120.12’ W; 1828 m mean elevation) during 2004–2008. The climate is characterized by warm, dry summers and cold, moist winters. Mean annual temperature is
Table 1

Pre-treatment (2004) and post-treatment (2008) stand conditions within 4-ha experimental plots on the Tahoe National Forest, California, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Slope (%)</th>
<th>Aspect ('</th>
<th>Crown cover (%)</th>
<th>QMD (cm)</th>
<th>SDIa</th>
<th>Trees (/ha)</th>
<th>Basal area (m²/ha)</th>
<th>P. ponderosa (%)b</th>
<th>P. jeffreyi (%)b</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 2004</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Untreated control</td>
<td>5.4 ± 0.7</td>
<td>308.9 ± 26.5</td>
<td>37 ± 4</td>
<td>34.0 ± 4.0</td>
<td>139.9 ± 34.9</td>
<td>247.1 ± 87.4</td>
<td>19.1 ± 4.2</td>
<td>83.3 ± 5.1</td>
<td>16.7 ± 5.1</td>
</tr>
<tr>
<td>Early season</td>
<td>8.3 ± 2.7</td>
<td>248.6 ± 20.8</td>
<td>41 ± 5</td>
<td>31.2 ± 2.6</td>
<td>173.8 ± 11.3</td>
<td>323.7 ± 61.4</td>
<td>23.5 ± 0.8</td>
<td>67.7 ± 17.3</td>
<td>32.3 ± 17.3</td>
</tr>
<tr>
<td>Late season</td>
<td>7.5 ± 2.1</td>
<td>224.6 ± 7.5</td>
<td>29 ± 4</td>
<td>37.3 ± 0.7</td>
<td>84.0 ± 8.3</td>
<td>111.2 ± 7.9</td>
<td>7.3 ± 1.3</td>
<td>56.7 ± 8.8</td>
<td>43.3 ± 8.8</td>
</tr>
<tr>
<td>B. 2008</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Untreated control</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>34.0 ± 4.0</td>
<td>139.8 ± 34.8</td>
<td>246.4 ± 86.9</td>
<td>19.1 ± 4.2</td>
<td>83.3 ± 5.1</td>
<td>16.7 ± 5.1</td>
</tr>
<tr>
<td>Early season</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>32.5 ± 2.2</td>
<td>160.5 ± 10.0</td>
<td>275.6 ± 45.3</td>
<td>22.1 ± 0.8</td>
<td>67.1 ± 17.5</td>
<td>32.9 ± 17.5</td>
</tr>
<tr>
<td>Late season</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>40.1 ± 0.8</td>
<td>78.6 ± 8.0</td>
<td>92.7 ± 6.3</td>
<td>11.8 ± 1.3</td>
<td>59.8 ± 10.6</td>
<td>40.2 ± 10.6</td>
</tr>
</tbody>
</table>

Values are means ± SEM. No significant differences were observed among means in any column/yr (df = 2,6; P > 0.055, all cases).

a QMD, quadratic mean diameter; SDI, stand density index.
b Based on numbers of trees.
c Unchanged.

~6.3 °C. Mean annual precipitation is ~80 cm [Fig. 1; at 39.22°N, 120.18°W; 1829 m elevation; Western Regional Climate Center] with most coming as snow between December and April. Stands were mechanically thinned from below in 1997 and 1998 leaving the residual stands relatively open and dominated by P. ponderosa and P. jeffreyi (Table 1), but a few (<1 tree/ha) incense cedar, Calocedrus decurrens (Torr.) Florin, white fir, Abies concolor (Gord. and Glend.) Lindl. ex Hildebr., and lodgepole pine, P. contorta Doug. ex Loud., were also present. Few activity fuels (logging residues) were present in 2005 (plots 2, 3 and 7). All prescribed burns were implemented. All litter, duff, and other small surface fuels (<2.54 cm diameter, 1- and 10-h fuels; cones excluded) were collected. Only fuels with a total length >0.5 m with large end diameter >5.0 cm were measured. For each qualifying log, the smallest and largest diameter within the strip plot, and total length within the strip plot to a minimum diameter of 2.54 cm were recorded. Mass was calculated using equations provided by Brown (1974, p. 18) incorporating specific gravity values obtained from van Wagendonk et al. (1996) for P. ponderosa and P. jeffreyi in the Sierra Nevada. Fuel consumption was calculated by subtracting the oven-dried weights of materials in post-burn quadrants from those of the pre-burn quadrants. Prior to burns, 10 high-registering thermometers were buried horizontally along the interface between the mineral soil and overlying organic layers in each burn plot (N = 60) to provide an estimate of peak soil temperatures. One thermometer was placed 1 m north of the center point of each 1-m² subplot. Thermometers were retrieved and temperatures recorded within 48 h of each burn.

2.3. Data collection

Pre-treatment data were obtained for each plot within five 0.081-ha circular subplots (N = 45) by conventional means: (1) number of trees (>8.9 cm dbh), (2) diameter at breast height (dbh, 1.37 m in height), (3) basal area, (4) tree species, (5) percent crown cover (by densitometer), (6) slope and (7) aspect. Subplots were permanently established with rebar. Ten 1-m² subplots (N = 60) were established in each burn plot with two associated with each 0.081-ha subplot (i.e., systematically placed 20.2 m from the center point) and divided into four equal (0.25 m²) quadrants. Two quadrants were destructively sampled before and two after burns were implemented. All litter, duff, and other small surface fuels (<2.54 cm diameter, 1- and 10-h fuels; cones excluded) were collected within 11 d of each burn, dried at 90 °C for 48 h, and weighed. Fuel consumption was calculated by subtracting the oven-dried weights of materials in post-burn quadrants from those of the pre-burn quadrants. Prior to burns, 10 high-registering thermometers were buried horizontally along the interface between the mineral soil and overlying organic layers in each burn plot (N = 60) to provide an estimate of peak soil temperatures. One thermometer was placed 1 m north of the center point of each 1-m² subplot. Thermometers were retrieved and temperatures recorded within 48 h of each burn.
Table 2

Weather conditions, fuels and measures of fire intensity and fire severity following early and late season prescribed burns applied to 4-ha experimental plots on the Tahoe National Forest, California, USA, 2005.

<table>
<thead>
<tr>
<th>Burn season</th>
<th>Wind speed (kph)</th>
<th>Fuel consumption (kg T/ha)</th>
<th>Fuel consumption (kg T/ha)</th>
<th>Fuel consumption (kg T/ha)</th>
<th>Fuel consumption (kg T/ha)</th>
<th>Fuel consumption (kg T/ha)</th>
<th>Fuel consumption (kg T/ha)</th>
<th>Soil interface temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>3.2 ± 0.9</td>
<td>49.1 ± 7.6 b</td>
<td>28.1 ± 7.9 a</td>
<td>42.2 ± 6.6 a</td>
<td>51.8 ± 11.3 a</td>
<td>31.1 ± 13.3 a</td>
<td>85.8 ± 4.9 b</td>
<td>86.8 ± 4.9 b</td>
</tr>
<tr>
<td>Late</td>
<td>2.4 ± 0.3</td>
<td>51.9 ± 5.6 a</td>
<td>48.1 ± 5.1 b</td>
<td>54.4 ± 6.5 a</td>
<td>51.9 ± 5.6 a</td>
<td>31.1 ± 13.3 a</td>
<td>85.8 ± 4.9 b</td>
<td>86.8 ± 4.9 b</td>
</tr>
</tbody>
</table>

Values are means ± SD.  
* Conditions at the field site immediately prior and during burning. Air temperature was 22.2 ± 0.3 and 10.4 ± 13.9 °C; relative humidity was 38.4 ± 1.1 and 61.7 ± 6.5 for early- and late-season burns, respectively.  
** Ten high-registering thermometers were buried horizontally along the interface between the mineral soil and overlying organic layers.  
*** Classes based on the timelag principle (Pyne et al., 1996).  
**** CKR, Cambium kill rating; values 0–4 based on the number of quadrants sampled per tree that contained dead cambium (Hood et al., 2007).  
#### Analyses

Primary variables of interest were the mean percentage of trees killed by (1) all causes (total mortality), (2) prescribed fire (direct mortality), and (3) bark beetle species (indirect mortality) by 10.2-cm diameter classes [10.2–20.2 cm (15.2 cm midpoint), 20.3–30.4 cm (25.4 cm), 30.5–40.5 cm (35.6 cm), 40.6–50.7 cm (45.7 cm), >50.7 cm (all trees); dbh]. Mortality was only attributed to bark beetles when burn severity rankings on individual trees were ≤ 3 (Fettig et al., 2008, 2010). A ranking of four indicates the tree was directly killed by prescribed fire, regardless of any evidence of bark beetle attack, as indicated by external measures of fire severity (i.e., charring of bark plates and fissures with substantial bark consumption). Therefore, a distinction is made between trees directly killed by prescribed fire and those predisposed by fire to bark beetle attack (Ganz et al., 2003). The experimental design was completely randomized with three treatments and three replicates per treatment (df = 2, 6). A
test of normality was performed and appropriate transformations were used when data deviated significantly from a normal distribution. We performed an analysis of variance on each response variable at \( \alpha = 0.05 \) (SAS Institute Inc., Cary, NC, USA). If a significant treatment effect was detected, Tukey’s multiple comparison test (Tukey’s HSD) was used for separation of treatment means requiring more than one comparison.

3. Results and discussion

3.1. Overall tree mortality

A total of 816 trees (9.9% of all trees) died during this 3-yr study, of which 71.6% (584 trees), 27.5% (224 trees) and 0.9% (8 trees) occurred on early season, late season and untreated control plots, respectively. These values represent mortality attributed to all sources (i.e., prescribed fire, bark beetles, pathogens and unidentified sources, and their many interactions). Significantly higher levels of tree mortality occurred following early and late season burns compared to the untreated control (all trees; \( F_{2,6} = 42.4, P < 0.001 \)), however no significant difference was observed between burn treatments (Fig. 2). For the largest trees (>50.7 cm dbh), significantly higher levels of tree mortality occurred on early season burns than the untreated control (\( F_{2,6} = 5.5, P = 0.044 \)), but for the smallest trees (15.2 cm dbh class) mortality was significantly higher on late season burns compared to the control (\( F_{2,6} = 8.3; P = 0.019 \)) (Fig. 2). For trees in the middle diameter classes, we only observed a significant treatment effect in the 35.6 cm dbh class in which higher levels of tree mortality occurred on late season burns compared to the untreated control (\( F_{2,6} = 5.8, P = 0.040 \)). No significant differences were observed between early and late season burns within any dbh class (Fig. 2). Overall, tree mortality was concentrated in the smallest dbh class for both early (\( F_{4,10} = 7.0, P = 0.005 \)) and late season burns (\( F_{4,10} = 9.8, P = 0.002 \)) (Table 3).

As a result of tree mortality, quadratic mean diameter increased while stand density index (SDI), trees/ha, and basal area declined for both early and late season burns, however no significant differences were observed among treatment means (\( P > 0.12 \), all cases). Effects were generally more pronounced for late season burns (Table 1). Slight shifts in tree species composition were observed for both early and late season burns, but not for the untreated control where tree mortality was negligible (Fig. 2).

3.2. Direct tree mortality

The majority (56.5%, 461 trees) of tree deaths was attributed to direct mortality resulting from prescribed burns, and was highly concentrated in the smallest dbh class (84.8% of all direct mortality; Fig. 3). Generally, larger trees are more fire-resistant (Peterson and Ryan, 1986; Harrington, 1993; Agee and Skinner, 2005; Thies et al., 2005; Sieg et al., 2006), particularly those species that have thick bark (Ryan and Reinhardt, 1988), which reduces cambium injury (Martin, 1963; Hood et al., 2008). Furthermore, larger trees tend to have higher crowns (i.e., heights to the base of the live crown) and greater heat sink capacities resulting in less fire-related injury (Ryan and Reinhardt, 1988), Regelbrugge and Conard (1993) reported decreased probability of post-fire mortality in P. ponderosa with increasing tree diameter and height in the central Sierra Nevada. However, Hood et al. (2008) found the predicted probability of dead cambium in P. ponderosa increased as diameter increased, but the relationship was reversed for all other tree species sampled in their study. Other authors have suggested that

Table 3

<table>
<thead>
<tr>
<th>Dbh class</th>
<th>Total mortality</th>
<th>Direct mortality</th>
<th>Indirect mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early season</td>
<td>Late season</td>
<td>Early season</td>
</tr>
<tr>
<td>15.2</td>
<td>21.6 ± 3.7 a</td>
<td>62.8 ± 18.8 a</td>
<td>11.0 ± 1.9 a</td>
</tr>
<tr>
<td>25.4</td>
<td>12.6 ± 5.7 ab</td>
<td>9.2 ± 2.5 b</td>
<td>7.4 ± 4.3 ab</td>
</tr>
<tr>
<td>35.6</td>
<td>3.1 ± 1.0 b</td>
<td>3.9 ± 1.1 b</td>
<td>1.5 ± 0.8 b</td>
</tr>
<tr>
<td>45.7</td>
<td>1.9 ± 1.0 b</td>
<td>1.1 ± 0.6 b</td>
<td>0.5 ± 0.2 b</td>
</tr>
<tr>
<td>&gt;50.7</td>
<td>3.2 ± 1.7 b</td>
<td>0.2 ± 0.6 b</td>
<td>0.4 ± 0.4 b</td>
</tr>
</tbody>
</table>

Means (±SEM) followed by the same letter within columns are not significantly different (Tukey’s HSD, \( P > 0.05 \)).
older *P. ponderosa* are more susceptible to mortality after fire than younger, mature trees (Kolb et al., 2007). Larger trees are more likely to die than smaller trees with similar levels of crown and cambium injury (Hood et al., 2007), perhaps because of greater basal duff accumulations resulting in increased fire duration and intensity, elevated levels of fine root injury, and reduced tree vigor, especially during periods of drought. In Arizona, McHugh and Kolb (2003) reported mortality 3 yr after fire was highest for trees with the smallest diameters (<20 cm dbh), which agrees with our study. Mortality decreased as diameter increased between 20 and 50 cm dbh as would be expected due to increasing bark thickness. However, mortality increased as diameter increased among the largest trees (>50 cm dbh). *P. ponderosa* died within 2 yr following prescribed burns compared with 19% mortality for smaller diameter trees. Other studies have reported similar trends described as a “U-shaped” distribution of *P. ponderosa* mortality by tree diameter (Kolb et al., 2007), which is not consistent with our study (Figs. 2 and 3) and others conducted in northern California (Schwilk et al., 2006; Fettig et al., 2008, 2010). Direct tree mortality was concentrated in the smallest dbh class for early season burns (*F*<sub>1,10</sub> = 6.7, *P* = 0.007), but no significant differences were observed for late season burns (*F*<sub>1,10</sub> = 2.6, *P* = 0.105) (Table 3), due to high levels of variation in the 15.2 cm dbh class.

We observed no significant differences in the amount of direct mortality between early and late season burns (all trees; *F*<sub>1,4</sub> = 0.3, *P* = 0.588) or within individual dbh classes (*P* < 0.12, all cases; Fig. 3). Late season burns are generally thought to be of greater intensity (Ryan et al., 1988; Skinner and Chang, 1996; Thies et al., 2005), and therefore presumably result in higher levels of tree mortality, particularly in smaller diameter classes. Our late season burns were implemented during cooler (~10 and 22 °C) and moister (~62 and 36% relative humidity) weather conditions than early season burns, but resulted in significantly higher levels of large (>100-h) downed woody fuel consumption and CKR (Table 2). Greater crown damage and bole char heights were observed following early season burns (Table 1), which may be influenced by pre-treatment stand density (Table 2). Substantial fuel consumption occurred following both early and late season burns (Table 2), and overall surface fuel loads were moderate (~39 t/ha, ≤10-h) for *P. ponderosa* and *P. jeffreyi* forests (Stephens, 2004). Mean maximum soil temperatures were ~81 and 88 °C for early and late season burns, respectively (Table 2). A temperature of 60 °C for 1 min is considered lethal to plant tissues (Hare, 1961), and it is therefore likely that heat injury occurred to some fine roots perhaps weakening trees and rendering them more susceptible to bark beetle attacks and/or fungal infections. Heating also caused significantly more cambium injury (CKR) in late season burns compared to early season burns, although injury was low for both treatments (Table 2).

Trees that died directly from prescribed burns had significantly higher levels of crown damage compared to all other trees following early season (*F*<sub>2,6</sub> = 63.5, *P* < 0.001; 80.6 ± 3.1 versus 40.8 ± 3.1%; mean ± SEM) and late season burns (*F*<sub>2,6</sub> = 9.4, *P* = 0.014; 51.9 ± 12.0 versus 17.4 ± 3.0%). However, no significant differences were observed for average bole char height between trees that died directly from prescribed burns and all other trees (*P* > 0.14, both cases). There were no significant differences between early and late season burns in crown damage or average bole char height on trees that died from direct fire effects (*P* > 0.08, both cases). Most researchers that have examined the effect of fire on mortality of conifers in the western USA have concluded that crown injury is the most important predictive variable (Fowler and Sieg, 2004). Recent work on *P. ponderosa* and *P. jeffreyi* in California found crown injury, cambium injury (CKR), dbh and presence of RTB attacks were important predictors of post-fire survivability (Hood et al., 2007).

### 3.3. Indirect tree mortality

Following prescribed fire, tree mortality may be immediate due to consumption of living tissue or heating of critical plant tissues, or can be delayed, occurring over the course of a few yr, as a result of fire injuries to the crown, bole or roots (Hood et al., 2007). In addition to direct mortality attributed to fire effects, bark beetles may attack and kill trees that were injured by fire, but that otherwise likely would have survived (Parker et al., 2006). Furthermore, these brood trees (i.e., those containing immature stages of bark beetles and attacking adults) may serve as a source of beetles and attractive semiochemicals (i.e., kairomones and pheromones) that attract other beetles into the vicinity resulting in additional levels of subsequent tree mortality (e.g., group kills resulting from WPB attacks were observed following spring burns). During our study, MPB (56 trees) and WPB (67 trees) were found colonizing *P. ponderosa*; and JPB was found colonizing *P. jeffreyi* (seven trees). We also found pine engraver (PE), *Ips pini* (Say) (137 trees), and, to a much lesser extent, *Orthotomicus* (=*Ips* latidens (LeConte) (85 trees) and emarginate ips, *I. emarginatus* (LeConte) (three trees) colonizing *P. ponderosa* and *P. jeffreyi*.

Some wood borers are attracted to fire (Evans, 1966), smoke (Wickman, 1964) and fire-injured trees (Rasmussen et al., 1996), but their contribution to tree mortality is largely unknown following mixed-severity wildfire (Rasmussen et al., 1996) or prescribed fire (Fettig et al., 2008). Some wood borers are regarded as forest pests. For example, California flatheaded borer, *Melanophila californica* Van Dyke, is known to cause tree mortality, particularly during extended periods of drought (Furniss and Carolin, 1977). McHugh et al. (2003) found wood borers were the most common insect found in trees following mixed-severity wildfires and prescribed fire in *P. ponderosa* forests in Arizona. Fettig et al. (2008) reported that wood borer attacks directly contributed to tree mortality [i.e., based on timing (yr) of crown fade following prescribed fire and absence of attacks by tree-killing bark beetles] in numerous fire-injured trees 2 yr after the application of prescribed fires in the northern Sierra Nevada, and that in the absence of such attacks tree mortality would likely not have occurred. However, evidence of such an effect was not observed in a second study conducted in the Southern Cascades of California (Fettig et al., 2010) or in this study.

The precise role of each bark beetle species in causing tree mortality on our experimental plots is uncertain. Fire-injured *P. ponderosa* and, to a lesser extent *P. jeffreyi*, are susceptible to colonization by several species of bark beetles. For example, Fettig et al. (2008) reported the application of prescribed fire resulted in significant increases in bark beetle-caused tree mortality (all species) and for WPB, MPB and engraver beetles (*Ips* spp.) individually in *P. ponderosa* forests in the northern Sierra Nevada. In our study, attacks by several bark beetle species were accompanied by those of other bark beetles within the same tree. Accordingly, in reference to WPB, MPB, and JPB, we attributed tree mortality to one of these species if evidence of colonization was found despite the potential existence of other bark beetle species. On occasion (14 trees), we found PE and *O. (ips) latidens* infesting the same tree and in these situations we attributed tree mortality to PE. Tree mortality was attributed to *Ips* spp. (including PE) only when evidence of WPB, MPB, or JPB colonization was absent. It is possible that bark beetles attacked the upper bole of trees above our sampling height that we therefore classified as dead due to prescribed fire effects on burned plots (Breece et al., 2008). On the other hand, *Ips* spp. are known to attack dying trees (i.e., they do not require succulent phloem to reproduce) and therefore it is possible that some mortality attributed to *Ips* attacks could have occurred in absence of these attacks.

We also found RTB colonizing many trees, both live and dead. Red turpentine beetle attacks are usually confined to basal portions...
of previously stressed, weakened, or dead and dying trees (Furniss and Carolin, 1977), or those under attack by other bark beetles, such as WPB (Fettig et al., 2004a). Attacks typically do not cause tree mortality in the absence of confounding factors. However, tree mortality was attributed to RTB in a 17-yr-old *P. ponderosa* plantation in northern California (Rappaport et al., 2001), for several trees in stands where logging residues were chipped and retained on-site in northern California (Fettig et al., 2006), and of *P. tabuliformis* Carrière in China where RTB was accidentally introduced (Li et al., 2001). Despite this, we did not attribute tree mortality to RTB attacks in this study.

A total of 355 trees (4.3% of all trees) were killed by bark beetles (all species) during this study. Overall, we observed no significant treatment effect in the amount of bark beetle-caused tree mortality (all trees; \(F_{2,6} = 4.3, P = 0.070\)) despite substantial differences in levels of bark beetle-caused tree mortality between burn treatments and the untreated control (Fig. 4). Indirect mortality attributed to bark beetle attack was concentrated in the smallest dbh class for late season (Fig. 4) and the untreated control (Fittig et al., 2003). McHugh et al. (2003) showed the amount of crown scorch (percentage) and consumption (percentage) volume collectively accounted for the majority of predictive capacity in their models to predict individual tree survival. The addition of dbh and presence of *Ips* beetles increased predictive power. Breece et al. (2008) concluded canopy damage from fire was a strong and consistent predictor of post-fire mortality of *P. ponderosa*, and that bark beetle attacks and bole char rating were less consistent predictors.

### 3.3.1. *Ips* spp.

As with direct mortality, the majority (82.0%) of bark beetle-caused tree mortality occurred in the smallest dbh class most of which was attributed to *Ips* spp. A total of 225 trees (2.7% of all trees) were killed by *Ips* spp. of which 95.6% occurred in the smallest dbh class. No *Ips*-caused tree mortality occurred in the 35.6 and >50.7 cm dbh classes (Fig. 5). Overall, we observed a significant treatment effect in the amount of *Ips*-caused tree mortality (all trees; \(F_{2,6} = 5.3, P = 0.047\)) and within the smallest dbh class (\(F_{2,6} = 10.7, P = 0.010\)) with significantly higher levels occurring on late season burns than the untreated control (Fig. 5). No other significant differences were observed (Fig. 5).

*Ips* spp. generally colonize slash, saplings and weakened trees or trees previously colonized by other bark beetle species (Kegley et al., 1997). Outbreaks are often short-lived, but increase in duration and extent when suitable host material is plentiful and populations...
grow sufficiently large to colonize apparently healthy trees. In our study, fewer larger trees (>20.3 cm dbh; 10 trees) were killed by *Ips* spp., but ~16% of all trees in the 15.2 cm dbh class died as a result of *Ips* attacks following late season burns. Ganz et al. (2003) studied the effects of prescribed fire on susceptibility of *P. ponderosa* and *P. jeffreyi* to bark beetle attack in two case studies in California, and reported >30% of pines were killed by PE the first yr following prescribed burns. Bradley and Tueller (2001) reported 36 of 389 pines were colonized by *Ips* spp. the yr following prescribed burns in the Lake Tahoe Basin of California and Nevada, USA. Furthermore, Fettig et al. (2008) reported the application of prescribed fire resulted in a significant increase in the proportion of pines (>19 cm dbh) killed by *Ips* spp. with ~99% of all *Ips*-caused tree mortality occurring on burned plots. Generally, *Ips* spp. colonize smaller trees (5–20 cm dbh; Kegley et al., 1997), and attack rates are negatively correlated with tree dbh in *P. ponderosa* (Kolb et al., 2006; Negrón et al., 2009).

In some areas, top killing of live pines by *Ips* spp. is common, but was not evident in our study. Breece et al. (2008) reported attacks by *Ips* spp. were more common in the upper bole than the lower bole following fire and increased by 3.7× for every 2 m increase in height on the tree bole. In their study, most attacks also occurred in the smaller diameter classes.

### 3.3.2. Western pine beetle

A total of 67 *P. ponderosa* (0.8% of all trees) were killed by WPB. Western pine beetle is a major cause of *P. ponderosa* mortality in portions of the western USA (Miller and Keen, 1960). Under certain conditions, the beetle can attack and kill apparently healthy trees of all ages and size classes. *Pinus ponderosa* is the only host of WPB present in these stands (Miller and Keen, 1960). Overall, we observed a significant treatment effect in the amount of WPB-caused tree mortality (all trees; *F* 2,6 = 5.4, *P* = 0.045) and within the smallest dbh class (*F* 2,6 = 28.1, *P* < 0.001). In both cases, significantly more WPB-caused tree mortality occurred on early season burns than the untreated control (Fig. 6), the latter in which no WPB-caused tree mortality occurred. While large numbers of WPB adults are active throughout much of the yr, flight activity peaks in June in *P. ponderosa* and *P. jeffreyi* forests (Fettig et al., 2004b; data from site ~166 km NNW at similar elevation), which likely explains the effect observed. A similar effect was observed for WPB following chipping of *P. ponderosa* in spring compared with the late summer (Fettig et al., 2006; DeGomez et al., 2008), and was linked to high concentrations of attractive volatiles released from chips during the major flight activity period.

About 43% (29 trees) of all WPB-caused tree mortality occurred on early season burns within the smallest dbh class which is surprising given the beetle's preference for larger diameter trees (50.8–81.3 cm dbh; Person, 1928), but agrees with other studies that evaluated the effects of prescribed fire on levels of bark beetle-caused tree mortality in northern California (Fettig et al., 2008, 2010). No WPB-caused tree mortality occurred following late season burns in the smallest dbh class (Fig. 6). McHugh et al. (2003) reported that WPB colonized only three of 222 trees following a prescribed fire in Arizona. Similarly, Sánchez-Martínez and Wagner (2002) detected no significant difference in the amount of WPB-caused tree mortality between managed (including prescribed fire) and unmanaged stands in Arizona, but others have established a link between fire-injury and the increased susceptibility of *P. ponderosa* to WPB attack (e.g., Miller and Patterson, 1927; Fischer, 1980).

### 3.3.3. Mountain pine beetle

A total of 56 *P. ponderosa* (0.7% of all trees) were killed by MPB. Mountain pine beetle occurs throughout British Columbia, Alberta, most of the western USA, and into northern Mexico, and colonizes several pines, most notably *P. contorta*, *P. ponderosa*, sugar pine, *P. lambertiana* Dougl., whitebark pine, *P. albicaulis* Engelm., and western white pine, *P. monticola* Dougl. ex D. Don (Furniss and Carolin, 1977). The role of MPB in *P. ponderosa* stands in California is usually secondary to that of WPB (Miller and Keen, 1960), particularly in larger diameter trees.

Overall, we observed a significant treatment effect in the amount of MPB-caused tree mortality (all trees; *F* 2,6 = 6.7, *P* = 0.029) and within the smallest dbh class (*F* 2,6 = 7.5, *P* = 0.023). In both cases, significantly more MPB-caused tree mortality occurred on late season burns than the untreated control (Fig. 7), which is different than the effect we observed for WPB. While large numbers of MPB are flight active throughout much of the yr, flight activity generally peaks in late summer and fall (August and October) in *P. ponderosa* and *P. jeffreyi* forests (Fettig et al., 2004b), which likely explains the effect observed. No MPB-caused tree mortality occurred in the untreated control within the three largest dbh classes (>30.5 cm), and none occurred in the 45.7 cm dbh class within any treatment (Fig. 7). Fettig et al. (2008) reported the application of prescribed fire resulted in significant increases in MPB-caused tree mortality.
except within the two largest dbh classes (>49.6 cm dbh). In their study, ~83% of all MPB-caused tree mortality occurred on burned plots. Fettig et al. (2010) reported similar results in the Southern Cascades where the amount of MPB-caused tree mortality was significantly greater following prescribed burns in the two smallest dbh classes (<39.3 cm dbh). Alternatively, others have found no effect (Rasmussen et al., 1996; McHugh et al., 2003; Elkin and Reid, 2004), particularly in P. contorta.

3.3.4. Jeffrey pine beetle

Few P. jeffreyi (seven trees) were colonized by JPB and therefore statistical analyses were not conducted. All JPB-caused tree mortality occurred on early (four trees) or late season burns. Jeffrey pine beetle can be a significant cause of P. jeffreyi mortality in portions of the Sierra Nevada (Furniss and Carolin, 1977), but several authors have reported few trees being colonized by JPB following burns (Bradley and Tueller, 2001; Ganz et al., 2003; Fettig et al., 2008). Maloney et al. (2008) found significant P. jeffreyi mortality following prescribed burns in mixed-conifer forests, but reported that JPB attacks occurred on only 11% of trees that died. While P. jeffreyi is moderately resistant to fire and shares many of the same adaptations to fire as P. ponderosa, it generally suffers less bark beetle-caused mortality following prescribed burns (Fettig et al., 2008). This may have more to do with the life history traits of JPB than any appreciable difference in the susceptibility of P. ponderosa and P. jeffreyi to bark beetle attack following similar levels of fire-injury. For example, JPB is univoltine and typically present in relatively low densities primarily breeding in slow growing trees of reduced vigor (Smith et al., 2009). Furthermore, a much larger complex of tree-killing bark beetles colonizes P. ponderosa than P. jeffreyi (Furniss and Carolin, 1977).

3.3.5. Red turpentine beetle

A total of 739 trees (8.9% of all trees) were colonized by RTB of which 76.5% survived, the remainder being classified as dead due to direct mortality attributed to fire effects or indirect mortality attributed to attacks by other bark beetle species. It is well-established that RTB colonizes fire-injured trees (Parker et al., 2006), particularly P. ponderosa (Fettig et al., 2008, 2010), and there is a concern that RTB populations could increase in fire-injured trees and attack adjacent apparently healthy trees (e.g., Ferrell, 1996; Ganz et al., 2003), or predispose trees to attack by other bark beetle species (Bradley and Tueller, 2001). Overall, significantly more trees were colonized by RTB on early and late season burns compared to the untreated control (all trees; F2,6 = 5.3, P = 0.047; Fig. 8). No significant difference was observed between early and late season burns (Fig. 8). A significant treatment effect was also observed for the 45.7 cm dbh class (F2,6 = 5.8, P = 0.039) in which significantly more trees were colonized by RTB on early season burns than the untreated control (Fig. 8), which differed with the 15.2 cm dbh class (Fig. 8). Fettig et al. (2008) reported >98% of pines that were attacked by RTB occurred on burned plots in the northern Sierra Nevada, but no tree mortality was attributed to these attacks. Few (10 trees) trees were attacked by RTB in the untreated control, and no attacks occurred within the two largest dbh classes in this treatment (Fig. 8). Based on Fettig et al. (2010), we feel any negative impacts by large numbers of RTB attacks following prescribed burns would have been captured during the 3-yr period.

Fettig et al. (2004a) reported that a single peak in RTB flight activity occurs in late May through early June in the Sierra Nevada. The beetle is capable of overwintering as an adult and there is often a period in early spring when large numbers of adults are captured. It is at this time that RTB is likely searching for viable hosts and therefore treatments such as prescribed burns (Fig. 8) and mechanical fuel treatments (Fettig et al., 2006) that might exacerbate attack typically result in higher levels of RTB attacked trees when implemented just prior to peak flight activity.

3.3.6. Root pathogens associated with bark beetles

We found Ophiostomatoid fungi belonging to the genera Leptographium and Sporothrix in root/root collar samples. The Leptographium isolates were morphologically consistent with descriptions of L. terebrantis S.J. Barras and T.J. Perry. Leptographium wagneri (W.B. Kendr.) M.J. Wingf., the cause of black stain root disease (BSRD), was not found nor was symptom consistent with BSRD infection. Black stain root disease is a serious pathogen of P. ponderosa and P. jeffreyi and is vectored by root feeding bark beetles (Schweigkofler et al., 2005). While soil and site disturbance is associated with inciting BSRD (Harrington and Cobb, 1988), little information is available on prescribed fire effects on occurrence or intensification of BSRD. In a preliminary report on BSRD in P. ponderosa, Otrosina et al. (2007a) reported higher levels of tree mortality in burned plots than in unburned plots, although occurrence of BSRD in burned plots declined to baseline levels 5 yr after treatment. Future studies should be conducted to more fully understand the effects of prescribed fire on this pathogen.

Of the 45 trees sampled, only eight were positive for either Sporothrix (two trees) or L. terebrantis. For either fungal genus, no seasonal burn treatment effects could be discerned in isolation frequency. Interestingly, no Ophiostomatoid fungi were isolated from control (unburned) samples or from trees having no cambium damage in burned treatments. The isolation of Leptographium is consistent with the incidence of RTB in this study (8.9% of all trees) and several Leptographium species are known associates of RTB, including L. terebrantis (Harrington, 1988). On the other hand, the isolation frequency in this study was surprisingly low. For example, in longleaf pine, P. palustris Mill., Otrosina et al. (2002) employed methods used in the present study and reported high isolation frequencies (>50%, all cases) of this group of fungi in roots following prescribed fire and fire + mechanical treatments (Ottosina et al., 1999). In the latter case, tree mortality was associated with root infection by L. terebrantis and L. procerum (W.B. Kendr.) M.J. Wingf. Relatively high frequencies (e.g., >75% for high severity wildfire) of L. terebrantis and L. procerum in lateral roots were also reported by Hanula et al. (2002) in P. palustris and slash pine, P. elliottii Englem., stands subject to mixed-severity wildfire. However, a follow up survey of these study plots (Hanula et al., 2002) detected no presence of Leptographium spp. in the roots 8 yr after the wildfire.
this mortality represents <1 tree/ha in these plots while manage-
trees (>50.7 cm dbh) were killed by WPB following early season

terebrantis associates of several conifer infesting bark beetles. While RTB is
(2007b). In green house pathogenicity tests,
216
beetle attacks on
P
plot 6; all 3 yr) to 3.7% (early season burn, plot 1; yr 1).

3.4. Temporal distributions of tree mortality

In our study, 38.1, 41.8 and 20.1% of total tree mortality
(≥20.3 cm dbh) occurred during the first, second and third yr,
respectively. Similar trends were observed for both direct and indi-
rect tree mortality. No significant differences in levels of total
mortality, direct mortality, or indirect mortality were observed
among yr (df = 2.24; P > 0.16, all cases). On an individual plot basis,
annual levels of tree mortality ranged from 0% (untreated control,
plot 6; all 3 yr) to 3.7% (early season burn, plot 1; yr 1).

Breece et al. (2008) reported that prescribed burns increased
bark beetle attacks on
P
ponderosa over 3 yr from 1.5 to 13% of
to 8.4%. Approximately 80% of all bark beetle-attacked trees were col-
ized during the first yr following the application of prescribed
burns. Eight and 12% were colonized during the second and third
yr, respectively (Breece et al., 2008). Fettig et al. (2010) reported
the amount of bark beetle-caused tree mortality was evenly dis-
tributed 2 and 4 yr after the application of thinning and burning treatments in the Southern Cascades. In their study, only one of
five analyses yielded a significant temporal effect on prescribed
burned units (i.e., burned and thinned + burned) in which signifi-
cantly higher levels of bark beetle-caused tree mortality occurred
2 yr after the application of prescribed burns in the smallest diameter
class (Fettig et al., 2010). It is possible that we have not captured all
tree mortality attributed to burn effects during this 3-yr period.

4. Management implications

Since 1999, ~800,000 wildland fires have burned ~28 million
ha in the USA (NIFC, 2009). Generally, fewer wildfires are affect-
ing larger areas at increased intensities and severities than during
prior decades. Such events emphasize the need for well-designed
silvicultural treatments to reduce their extent and severity. We
demonstrated that significantly higher levels of tree mortality (all
sources) occurred following early and late season burns com-
pared to the untreated control, however no significant difference
was observed between burn treatments (all trees; Fig. 2). Most
of the mortality was concentrated in the smallest diameter class
(<20.2 cm dbh, Table 3). For the largest trees (>50.7 cm dbh), sig-
nificantly higher levels of tree mortality occurred on early season
burns than the untreated control (F2,6 = 5.5; P = 0.044), most of
which resulted from indirect mortality attributed to bark beetle
attacks (Fig. 4), specifically WPB and MPB (Figs. 6 and 7). Ten large
trees (>50.7 cm dbh) were killed by WPB following early season
burns, including the largest in our study (101 cm dbh). However,
this mortality represents <1 tree/ha in these plots while manage-
ment standards recommend 4.9 and 7.4 snags/ha (with a minimum
dbh of 46 cm) in
P
ponderosa and mixed-conifer forests in portions of the southwestern USA, respectively (Ganey, 1999; Stephens,
2004). In the nearby Lake Tahoe Basin old-growth forest struc-
ture is reported to have a minimum of 5 snags/ha that are >76 cm
dbh (Barbour et al., 2002). Stephens (2004) reported ~4 snags/ha
for
P
jeffreyi mixed-conifer forests in the Sierra San Pedro Martir
National Park, Mexico, an area that has not experienced systematic
fire suppression. In our study, WPB created most large-diameter
snags (11 of 15) generated during the 3-yr period. Furthermore,
we found no large-diameter snags that had been recently killed
(i.e., within 2 yr by presence of crown fade) during our initial cen-
sus. Few (<1/ha) older snags (>2 yr) were observed, suggesting that
these snags were, and likely will be, snag deficient for some time.
To that end, while some forest managers may be concerned by lev-
els of WPB-caused tree mortality in large-diameter trees following
early season burns, this mortality was not extensive and increased
snag densities toward target thresholds. Snags are important nest-
ing, roosting and foraging habitats for a variety of wildlife (Scott
et al., 1977; Bull et al., 1997). Many bird species exhibit a pref-
erence for larger (>50 cm dbh) and taller (>15 m in height) snags
(Laudenslayer, 2002; Lehmkuhl et al., 2003).

Precipitation patterns were normal during this study (Fig. 1)
and overall bark beetle activity levels were considered low to
moderate (USDA Forest Service, 2006, 2008). Furthermore, stand
densities in our study were low to moderate for
P
ponderosa
and
P
jeffreyi forests (10.4–25.5 m2/ha on an individual plot basis.
Table 1; Youngblood et al., 2004). Factors such as stand density,
tree diameter and host density are consistently identified as pri-
mary attributes associated with bark beetle infestations (reviewed
by Fettig et al., 2007). In this context, we caution the reader that
the amount of indirect mortality attributed to bark beetle attacks
in this study may be a conservative estimate, particularly in com-
parison to the application of these treatments in more dense stands
or during extended periods of drought.

A primary objective of using prescribed fire in
P
ponderosa and
P
jeffreyi forests is to reduce surface fuel loadings and densities
of small trees (e.g., <20.2 cm dbh) that serve as ladder fuels and
permit surface fires to become crown fires, while limiting undesir-
able levels of mortality within the larger diameter classes. A second
objective is to increase the relative proportion of fire-tolerant tree
species such as
P
ponderosa and
P
jeffreyi. However, this objective is
of limited relevance in the current study as stands were almost
pure
P
ponderosa and
P
jeffreyi (Table 1). In our study, early and late
season burns were equally effective at reducing fine surface fuels
(≤10-h fuels) and ladder fuels (i.e., small trees that provide vertical
continuity between surface and canopy fuels; Fig. 2), but late season
burns were more effective at reducing large downed woody fuels
(>10-h fuels) (Table 2). Few meaningful differences in levels of indi-
rect tree mortality attributed to bark beetle attack were observed
between early and late season burns. We conclude that late season
prescribed burns may be more effective at achieving overall man-
agement goals, but that early concerns regarding increased levels
of indirect tree mortality following early season burns are unwar-
ranted during the conditions under which this study was executed.
Further research is necessary to determine how early and late sea-
son burns would achieve the objectives described above under different site and stand conditions (e.g., under high stand densities)
where the potential for more severe tree injuries is greater.

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