Seasonal fire effects on mixed-conifer forest structure and pine resin properties

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This is to certify that I have examined this copy of a master's thesis by

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and have found it complete and satisfactory in all respects,
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-DP

Introduction

Fire exclusion during the 20th century is recognized to have caused long-lasting and profound effects on the landscape. Dry forest types, with historic conditions of widely-spaced trees above an herbaceous understory, are currently densely stocked with smaller trees and underbrush. Heavy fuel loads of litter and woody debris clutter the forest floor, as the surface fires that kept them in check have been all but eliminated (Covington and Moore 1994; Pyne 1980; Carle 2002; Agee 1993). These factors, combined, have led to the modern risk of stand-replacing fires, which has reached crisis condition in many areas.

In the mid- 20th century, as evidence mounted linking fire exclusion to increased fire hazard, researchers began calling for the restoration of the role of fire in American forests (Carle 2002). The National Park Service was one of the earliest agencies to embrace the new paradigm, adopting policies of prescribed burning and wildland fire use as early as the 1960's (Butts 1985). Other public agencies followed suit, gradually shifting fire policies from a singular focus on suppression to one of fire management (Carle 2002). In addition to fire use, structure-based prescriptions (Agee and Huff 1986) using mechanical thinning began growing in popularity, especially near developed areas, where public safety and air quality issues restrict the desirability of prescribed fire.

Crater Lake National Park, in southern Oregon, has a modest yet active prescribed burning program dating back to the 1970's. Vegetation in the southeastern region of the park consists of old-growth mixed-conifer/ponderosa pine (*Pinus ponderosa* Dougl ex

Laws) forest with a historic low- to mixed-severity fire regime (McNeil and Zobel 1980), representative of widely distributed mixed-conifer types in western states. Other than small areas recently treated with prescribed fire, suppression efforts have effectively excluded fire since 1902, when the park was created. These forests are currently in declining health due to vigorous growth of shade-tolerant underbrush, especially white fir (*Abies concolor* (Gord. & Glend.)Lindl.) (McNeil and Zobel 1980). The broad goal of fire management remains to restore these forests to healthier conditions through the use of fire, with species compositions and densities closer to historic benchmarks. Stand objectives of the burning program include reducing post-settlement tree density, maintaining dominant trees (especially ponderosa pines), and reducing fuel loads.

Following the initial experimental burns at Crater Lake in the 1970's and '80's, however, it became clear that increased mortality was occurring among older dominant ponderosa pines. These trees were supposedly fire resisters (Agee 1993), with thick bark and high crowns that should have protected them from the relatively mild heat of prescribed burns. Mortality, which occurred for several years after burning, was associated with damage to fine roots and crown scorching, and was often ultimately caused by attacks by bark beetles. This problem has raised serious questions about the appropriateness of prescribed burning for restoration purposes in this ecosystem (Agee 2003b).

Interactions between bark beetles and fire are beginning to be addressed (e.g. McHugh et al 2003; Feeney et al. 1998; Santoro et al. 2001), but are still poorly understood. While there has been documented evidence for decades that fire can increase bark beetle susceptibility (e.g. Miller and Keen 1960), this interaction has yet to be explained at a physiological level or widely applied to management prescriptions. Considering the importance of both fire and bark beetles in the ecology and managementof dry forest types, this is a serious concern.

Literature Review

Fuels management

Fuel reduction to limit wildfire hazard is probably the most common objective of management burning programs (Biswell et al. 1973; Martin 1990), and a major emphasis of current federal programs aimed at public safety and resource protection. As the only controllable factor of fire behavior triangle – weather and topography being outside the range of human influence (Martin 1990) – forest fuels are of major interest to land managers.

In low-severity fire regimes, fuels buildup due to fire exclusion has been recognized as a concern for decades. In central Oregon, Weaver (1959) presented early evidence for fuel buildup and increased fire hazard in pure ponderosa pine stands. Slightly higher in elevation and lower in latitude, the “panhandle” region of Crater Lake National Park consists of a ponderosa pine/mixed conifer forest in a similar state of fuel accumulation and declining health (McNeil and Zobel 1980), although recent restoration burning has sought to address the problem (Thomas and Agee 1986; Swezy and Agee 1991). Thomas and Agee (1986) measured a 67% reduction in dead and down fuels following summer burning; they estimated a post-fire fuel increase from fire-killed trees, however, limiting the predicted fuel reduction to 29% below pre-burning levels. Spring burning in ponderosa pine stands on the nearby Fremont National Forest, OR (Busse et al. 2000) resulted in immediate fuel reductions averaging 41% of pre-burn loads. In the southwestern US, fuel reduction from restoration burns has typically been high: in

Arizona ponderosa pine stands, Sackett (1980) measured post-fire fuel reductions of 65% and 43% following fall burning in two separate study areas, while Weaver (1952) reported reductions of 55 to 80% of woody fuels and duff from an early series of burns in Arizona. It should be noted that the proportions do not tell the full story, as southwestern ponderosa pine forest fuel loads are typically lower than those in northwestern mixed-conifer stands.

As Fernandes and Botelho (2003) have pointed out, quantitative data on thresholds for fuel reduction effectiveness is lacking, and fuel reduction treatment effects may be short-lived. It is therefore unclear how often "statistically significant" study results translate into real fire hazard reduction. Nonetheless, emerging studies offer considerable evidence that both burning and thinning do appear potentially effective in reducing subsequent wildfire severity in ponderosa pine forests (Pollet and Omi 2002; Stephens 1998; van Wagtendonk 1995; see Fernandes and Botelho 2003 for a review). In sum, prescribed burning appears effective in reducing fuel loads in ponderosa pine stands, although to what degree these reductions will significantly alter fire hazard, or how long the treatment effect will last, is stand-dependent and difficult to predict.

Fire and vegetation management

In addition to fuel reduction, objectives of restoration burns often include reducing small tree density and favoring fire-exclusion vegetation (Biswell et al. 1973). At Crater Lake, prescribed burning successfully reduced understory tree density, although considerable mortality of older trees also occurred (Thomas and Agee 1986), as will be further discussed below. Understory vegetation cover in fire-excluded forests is assumed to be lower than historic cover, due to the effects of resource competition from encroaching trees (McNeil and Zobel 1980; Sackett et al. 1996; Cooper 1960). Prior to most research, it was believed that understory species richness and cover should increase following burning due to increased resource availability; in practice, studies have shown highly variable responses of understory plants to fire (e.g. Borsting 2002). In addition to the effects of fire on competing vegetation, individual species will respond differently to the effects of fire itself. Vegetation in ecosystems with short fire-return intervals have various adapted strategies for persisting during or returning quickly following fire (Kauffman 1990; Agee 1993). Some typical fire adaptations classify species as fire resisters (mainly trees with thick bark), endurers (species that sprout following fire), or evaders (such as species whose seeds germinate following fire) (Agee 1993). Therefore, prescribed burning may increase understory diversity and cover overall, but some species will clearly be favored at the expense of others. McNeil and Zobel (1980) note that despite classification as a short-interval fire regime, Crater Lake's "Panhandle" fire history reflects some areas with extended fire-free periods (> 40 years in some places) prior to fire exclusion; the authors suggest that longer recovery periods may be important for the persistence of vegetation species with older reproductive ages, for instance.

A major vegetation concern of prescribed burning is that fire will encourage alien or invasive species. Research in northern Arizona ponderosa pine stands shows that following prescribed burning (Sackett et al. 1994) and wildfires (Crawford et al. 2001), alien species were significantly more abundant in burnt areas compared with controls or pre-burn abundances. Griffis et al. (2001) found that alien species richness and abundance showed very strong increases following an Arizona stand-replacing wildfire, while only alien species richness increased (and much more modestly) following thinning and burning treatments, relative to unmanaged control stands. The presence of alien species tends to run counter to typical ecological restoration goals (Friederici 2003, Frelich and Puettman 1999), making post-fire increases in aliens a potentially serious drawback of prescribed burning.

Other studies closer to southern Oregon have shown lesser dramatic effects to understory communities following burning. Busse et al. (2000) reported somewhat increased graminoid cover and reduced shrub cover in burned plots, although on the whole no significant changes to understory composition relative to controls. Borsting (2002) reports that 1 to 4 years after thinning and burning in northern California mixed-conifer forest, burned plots showed lower vegetation frequency and richness than similarly treated unburnt plots, although this was likely a result of plant consumption during the recent fires.

Overall, it is likely very difficult to predict understory species responses to burning: fire effects and post-fire regeneration will both vary according to the characteristics of the fire (intensity, season, behavior, patchiness, etc.), the time and nature of previous disturbances, site characteristics, proximity to surviving remnant vegetation or the existence of burn refugia, and other factors. Furthermore, as understory communities can vary tremendously by site, results of a particular study may be only relevant within narrow geographic and ecological confines. Effects of prescribed burning on understory communities in mixed-conifer forests at Crater Lake have not been documented prior to this study.

Old-growth pine mortality

Old-growth ponderosa pines are considered highly resistant to low-intensity fire (Biswell et al. 1973; Agee 1993), and maintaining these ecosystem elements was one of the primary objectives of the burning program at Crater Lake. However, initial prescribed burns at Crater Lake during the 1970's and 1980's suffered from high mortality of large pines (Thomas and Agee 1986; Swezy and Agee 1991). While some studies show positive ponderosa growth following prescribed fire (Weaver 1959; Cooper 1960; Covington and Sackett 1992), other studies report negative effects (Swezy and Agee 1991; Busse et al. 2000). Conflicting results on post-fire ponderosa performance arise because of the tradeoffs inherent in prescribed fire: beneficial effects of reduced competition and increased nutrient availability are tempered by fire damage to trees' roots, crown, and cambial tissue (Saveland and Bunting 1988). Thus, if trees are able to quickly recover from burn effects, they will often flourish in the highly favorable growing conditions; recovery, however, may be slow enough (or nonexistent) such that the "window of opportunity" to trees is lost.

Mortality following 1970's and 1980's burns at Crater Lake was higher in early season burns (37.6 % and 31.6 %) than in late season burns (12 %) or controls (6.6%) and appeared to be strongly related to crown scorch and root heating, the latter magnified because of shallow rooting depths in the nutrient-poor pumice soils (Swezy and Agee

1991; McNeil 1975). Thirteen years after a series of summer and fall burns (Thomas and Agee 1986), Agee (2003b) reported 36% and 17% mortality of larger sugar (*P. lambertiana* Dougl.) and ponderosa pines, respectively, compared with 10 and 14% mortality of the two species in control areas (differences between treatments and controls were not statistically significant for ponderosa pine, however, perhaps due to small sample sizes). Elsewhere, significant large-pine mortality has also been documented. Harrington (1993) found higher ponderosa mortality following spring and summer burns in Colorado compared with autumn burns, with most mortality occurring during the first year after burning. Sackett and Haase (1998) found over 40% of accumulated mortality of pre-exclusion ponderosa pines following 20 years of mixed-interval fall burning in Arizona, compared with about 15% mortality in control plots. McHugh and Kolb (2003) found considerable large-pine mortality 3 years after three different Arizona fires, where mortality was most strongly correlated with crown damage and bark beetle attack indices.

Some authors have suggested that raking away fuels or thinning stands before burning can help increase post-burn ponderosa pine growth and survival (e.g. Feeney et al. 1998). At Crater Lake, mechanical thinning has not been attempted, although litter and duff raking did not appear effective for this purpose, possibly because exposed fine roots were killed, leading to moisture stress, presumably merely replacing one source of stress (fire) with another (root death) (Swezy and Agee 1991). Other researchers have also observed increased mortality following raking where heavy duff layers are present (Timothy Duck, Utah BLM, personal communication). The technique of fuel raking has been used elsewhere, however, with and without mechanical thinning, with positive correlations with post-fire tree survival (Feeney et al. 1998; Fulé et al. 2001).

In sum, prescribed burning in untreated ponderosa pine stands may have negative effects on large-pine survivorship, at least until fuel levels and competing vegetation densities have been reduced by multiple low-intensity burns. In particular, higher mortality appears correlated with growing-season burns, high levels of root damage and crown scorch, and post-fire bark beetle attacks (McHugh and Kolb 2003; Swezy and Agee 1991; Harrington 1993). Success in maintaining old-growth ponderosa pines following prescribed burning, a frequent objective in restoration burns, remains uncertain.

While guidelines for estimating mortality due to fire damage are now common (Harrington 1993, Dieterich 1979, Wagener 1961), mortality of dominant ponderosa pines has been observed to continued for several years following burning (Agee 2003b; McHugh and Kolb 2003). Evidence suggested that second-order effects from insects, particularly *Dendroctonus* bark beetles, were important contributors to mortality. Losses of old-growth pines from prescribed fire are therefore attributable to both direct mortality from burning as well as subsequent bark beetle attacks on fire-weakened trees.

Fire – bark beetle interactions

At Crater Lake, the western pine beetle (WPB), *Dendroctonus brevicomis*, was responsible for post-fire mortality of many old-growth ponderosa pines. Other beetle species whose effects may have increased after burning include *Ips* species (*I. pini*, *I.*

paraconfusus) and turpentine beetles (*Dendroctonus valens*), the latter not generally considered a primary killer of ponderosa pines.

A successful WPB attack on a host tree follows a well-studied sequence: *Dispersal and selection* - Adult beetles initially disperse by flight, probably randomly. When a suitable host is located (old, weakened, or moribund ponderosa pine), beetles immediately begin feeding and nesting activities in the bark, releasing powerful attractant pheromones into the air. *Concentration* - Other beetles arrive, lured by the pheromone, and begin feeding and nesting; anti-aggregant pheromones are eventually released to discourage additional beetles from the focus tree when it is nearing carrying capacity. *Termination* - Host tree is killed by girdling and fungal intrusions; larvae develop, emerge and disperse anew (Moeck et al. 1981; Wood 1982; Raffa et al. 1993; Miller and Keen 1960).

Most of these steps are similar for other bark beetles species and their host trees. However, inter-specific differences exist, and broad generalizations have often proved incorrect: for instance, host species (both within and outside the *Pinus* genus) differ in resin production and anatomy (Phillips and Croteau 1999), primary attraction (see below), and induced responses to wounding (Lewisohn et al. 1991), while beetle species differ in numerous aspects of basic biology and life history, such as the number of larval generations spent in the phloem (Wood 1972). Thus, findings on other species of beetles or host trees may or may not apply to ponderosa pines and its insect parasites.

Following the Crater Lake burns, bark beetle-caused mortality in ponderosa pines increased, relative to unburnt trees (Swezy and Agee 1991; Thomas and Agee 1986).

Because of the effects of aggregant pheromones released during a successful initial attack, one of two possibilities is therefore implied (or both): following burning *1*-there were more initial attacks or *2*-there were similar numbers of attacks, but more were successful. The former possibility refers to so-called primary attraction (Moeck et al. 1981), the phenomenon of beetles being attracted from afar to chemical cues (kairomones) emitted by potential host trees.

Primary attraction is a contentious subject. While it is clearly a factor in the dispersal of some beetle species (Wood 1982; Gara et al. 1984), extensive experimentation has not shown any primary attraction to ponderosa pines from any of its primary (tree-killing; Wood 1982) bark beetle parasites, western pine beetles (Moeck et al. 1981) or mountain pine beetles (*D. ponderosae* Hopkins), nor from *Ips* species (which are usually considered secondary beetles) (Erbilgin and Raffa 2000; Wood 1982). The red turpentine beetle, *D. valens*, is mildly attracted to some ponderosa resin monoterpenes (Hobson et al. 1993; Erbilgin and Raffa 2000), but is generally not considered lethal to its host trees (Furniss and Carolin 1977; but see Ganz et al. 2001). If tree-killing bark beetles are attracted to olfactory cues in ponderosa pine volatiles, it is a very weak attraction that has not been detected by modern research techniques (Wood 1982).

If primary attraction is not a factor in WPB dispersal, then we cannot assume that higher beetle-related ponderosa mortality following prescribed fire is due to a greater *number* of initial beetle attacks; rather, a higher *proportion* of these initial attacks must be successful. Following a successful initial attack, of course, pheromones lure in many other beetles in a mass attack, the result of which is usually the death of the host tree (Miller and Keen 1960). Our focus therefore turns towards the ability or inability of individual trees to mobilize defenses against attacking beetles.

Oleoresin exudation and beetle resistance.

Resin, or oleoresin, stored in bark and sapwood ducts in most pines, provides their main defense against insects and other pathogens (Phillips and Croteau 1999; Miller and Keen 1960). Resistant ponderosa pines repel beetles via their resin, in 3 ways: physically (ejecting or smothering beetles; Miller and Keen 1960), chemically (through resin toxicity; Smith 1975), or by preventing nesting activities and reproduction (Raffa et al. 1993). In ponderosa pine, more resistant trees tend to have higher overall resin flows, resin flows that persist for longer following wounding, and higher proportions of certain chemicals (limonene) in their oleoresin (Smith 1975; 2000). Short-term injury-induced resin production, such as occurs in grand fir (*Abies grandis*) has not been found to be significant in ponderosa pine; most or all resin is pre-formed and stored in ducts (Lewisohn et al. 1991). The longer-term resin response of ponderosa pine to injury has not been studied, and it is not known whether resin defenses in subsequent seasons are affected by disturbances such as low-intensity fire. In other pine species, however, there is evidence of increased long-term (> 1 year) resin production following physical injury (e.g. Nebeker and Hodges 1983; Fredericksen et al. 1995; Kozlowski and Pallardy 1997).

The measurement of pine resin defenses has been a topic of debate for half a century or more. Several studies in Europe (reviewed in Vité 1961) first established a link between oleoresin exudation and environmental conditions, and observed that resin exudation was important for defense against insects. Schopmeyer et al. (1954) first suggested that Poiseuille's law of liquid flow through capillaries could be applied to oleoresin flow through the epithelial cells lining resin ducts, while Bourdeau and Schopmeyer (1958), working on slash pine (*Pinus elliottii*), suggested that oleoresin exudation pressure (OEP) could be directly measured using manometric techniques and that the pressure-viscosity ratio was related to oleoresin yield, or flow. Vité (1961) then conducted an extensive investigation into OEP and water relations in ponderosa pine using a hydrostatic pressure gauge technique; he concluded that "as an expression of both the water balance of the tree and its oleoresin flow, the oleoresin exudation pressure appears to be a dependable indicator of the physiological condition of a ponderosa pine and therefore its resistance or susceptibility to bark beetle infestation." (Vité 1961: 62) This assertion was tested by Vité and Wood (1961), who found that mature ponderosa pines with low OEP that were attacked by western pine beetles or mountain pine beetles (*Dendroctonus ponderosae*) tended to succumb to those attacks more often than pines with higher OEP.

A period of considerable interest in OEP studies followed, but with mixed results. Wood (1962) found that the beetles *Ips paraconfusus* were unable to infest ponderosa pines until their OEP had declined to zero through felling. Stark (1965) reported that no relationship was found between western pine beetle mortality and pre-dawn OEP in nearly 700 ponderosa pines in California. As OEP varied considerably throughout the day, it was usually measured at dawn, when it was highest (Vité 1961; Vité and Wood

1961). Western pine beetles, however, are known to fly during the afternoon (Gara and Vité 1962), as was noted by Stark (1965), raising doubts about the appropriateness of pre-dawn OEP measurement for assessing beetle susceptibility.

Several variations and refinements in methods for measuring OEP followed (e.g., Bushing and Wood 1964; Helseth and Brown 1970), and direct measurement of oleoresin flow rate (OEF) was proposed as a potential measure of beetle susceptibility (Mason 1971). Proponents of OEF measurement claimed that it was an actual indicator of oleoresin production, rather than merely showing the state of the oleoresin (as was the case with OEP; Mason 1971). Hodges and Lorio (1971), working on loblolly pine (*Pinus taeda*) found that OEP was significantly related to phloem water content and water pressure, but not to OEF. They suggested that this was related to differences in resin viscosity (which is genetically controlled and highly variable).

A thorough discussion of the OEP-OEF debate is provided by Lorio (1994), who concludes that while neither OEP nor OEF is apt to truly represent bark beetle resistance, OEF appears to be a superior method to OEP. He also suggests that a further reason why the two measures have not been found to be experimentally related could be because when the epithelial cells lining resin ducts are at high turgor pressure, they could actually partially close off the ducts and impede the flow of resin from a wound (Lorio 1994: 88-89). In any case, over 50 years after the first experiments in measuring conifer resin defenses, evidence suggests that a tree's OEP may indicate water balance (Lorio 1994; Vité 1961; Hodges and Lorio 1971), but not resin production or storage. Notwithstanding the influence of droughts on beetle attacks (Miller and Keen 1960), ponderosa pine resistance or susceptibility to bark beetles is still believed to be determined by resin quantity and chemical composition (Smith 1975, 2000). OEF is therefore the current method of choice for assessing bark beetle resistance in pines. OEF measurement techniques typically involve volumetric comparison of emergent resin from drilled or cut bole wounds over some period of time, often 24 hours (e.g. Feeney et al. 1998; Wallin et al. 2003).

The current knowledge of bark beetle-ponderosa pine dynamics is certainly not complete, but it has reached an advanced level of understanding. However, when we include the added complication of highly dynamic host responses (in this case due to the effects of fire), the current state of knowledge is much more limited.

Study Objectives

This study examines the ecological effects and forest health and management implications of initial post-exclusion restoration burning in Crater Lake mixed-conifer forest, broadly comparing spring and fall burning effects on a number of forest characteristics. The response variables measured were forest fuels, overstory vegetation structure, mortality of large ponderosa pines, and ponderosa pine resin properties. The latter were evaluated by measuring OEP and OEF on a subset of the pine population, before and several times after burning, to monitor the trees' ongoing susceptibility to bark beetle attacks and examine the relationship (if any) between beetle-caused pine mortality and reduced host defenses. Through this study, I hoped to be able to offer some critical evaluation into process-based restoration in this ecosystem, both from the broad perspective of forest structure as well as with a more focused ecophysiological approach, by examining the interactions between fire and bark beetle dynamics.

Methods

Study area

This study took place in Crater Lake National Park, OR. An unlogged and previously unmanaged (but for fire exclusion) area of approximately 67 hectares was selected at approximately 42° 48’N, 122°5’ W, along the southern boundary of the park adjacent to US Highway 62 (Figure 1). Elevation varied very little in the area, with a slight grade between about 1460 m (4800 ft) and 1550 m (5100 ft), with very limited topography and no slopes steeper than 2%. Due to its high elevation and position directly on the Cascade crest, the area receives heavy snowfall in winter, and does not usually melt out entirely until mid-June.

Pre-treatment forest structure in the study area was typical of fire-excluded stands in the mixed-conifer zone (Franklin and Dyrness 1973), near the zone’s upper elevation limit. Dominant trees include ponderosa pine, white fir (*Abies concolor*), Shasta red fir (*Abies magnifica* var. *shastensis*), and lodgepole pine (*Pinus contorta*); other species present consisted of sugar pine (*Pinus lambertiana*), western white pine (*Pinus monticola*) and mountain hemlock (*Tsuga mertensiana*), with individuals scattered throughout the stand; there was also one small patch of trembling aspen (*Populus tremuloides*). Douglas-fir (*Pseudotsuga menziesii*) was present just south of the study area, at slightly lower elevations, although no Douglas-fir individuals were actually seen in the study area. Woody fuels in the area consisted of a heterogeneous mosaic of fuel models 8, 9 and 10 (from Northern Forest Fire Laboratory fuel models; Albini 1976).

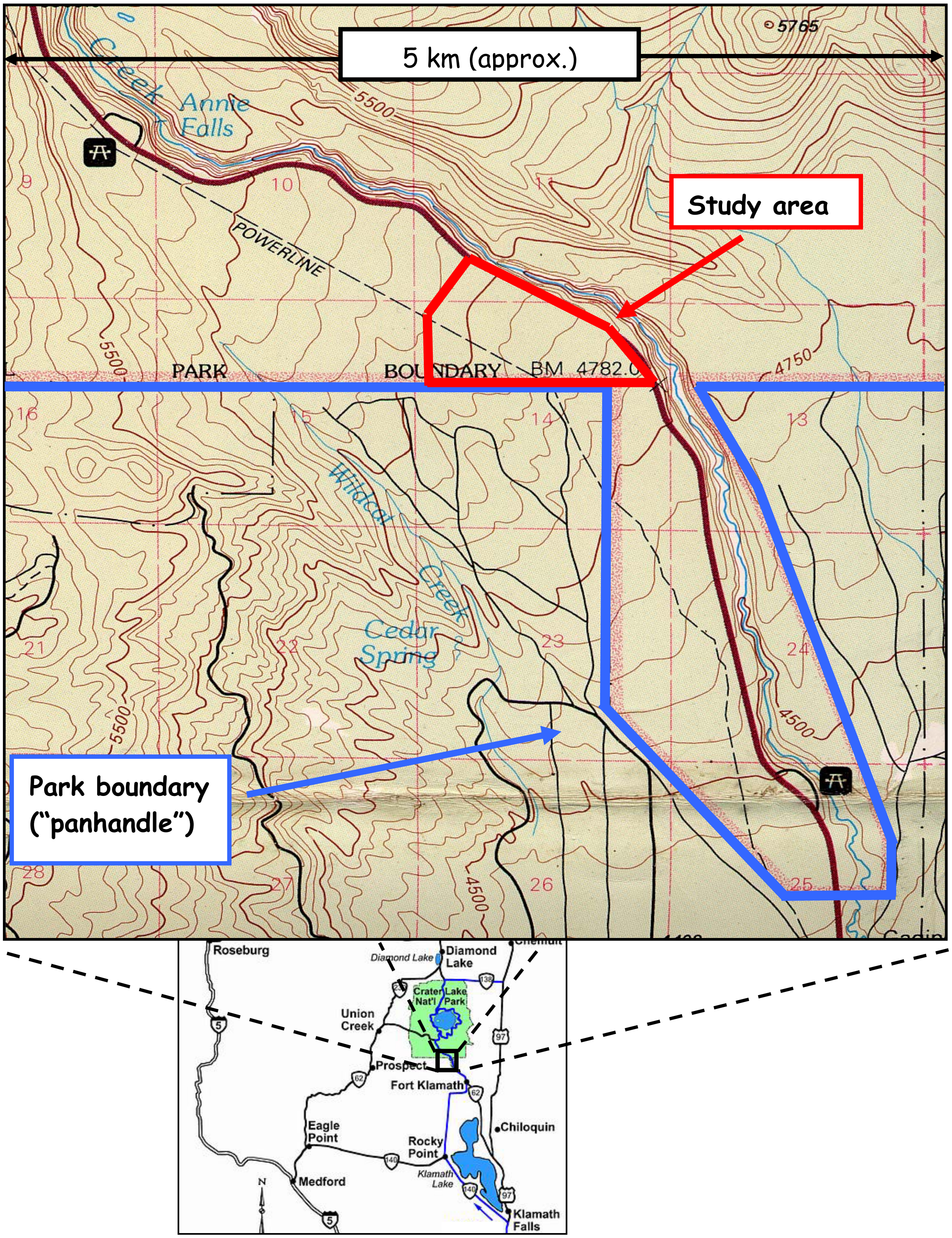


Figure 1. Study area location, along the southern boundary of Crater Lake National Park, Oregon.

McNeil (1975) describes the study area in its entirety as being composed of a few different but closely-related plant communities. All of these contain some amount of ponderosa pine in the overstory and considerable white fir in both the overstory and understory. Red fir, lodgepole pine and other trees varied in importance. Dominant understory species in these communities before burning included prince's pine (*Chimaphila umbellata*), one-sided pyrola (*Pyrola secunda*), manzanita (*Arctostaphylus nevadensis*), snowberry (*Symphoricarpus mollis*), snowbrush (*Ceanothus velutinus*), sedge species (*Carex pensylvanica* and other *Carex* sp.), and a number of others. While forest structure in the study area was very heterogeneous overall, understory diversity was generally low, likely due to the paucity of light reaching the forest floor. The area was historically characterized by a low to mixed-severity fire regime (Agee 1993). Fire-return intervals for the study area vary between 12.8 and 40 years, with a mean interval of 21.1 years (calculated from McNeil and Zobel 1980).

The study area was subdivided into 24 experimental units, with areas between 1.7 and 4.1 hectares (average of 2.8 ha). Units were randomly selected for spring burning (8), fall burning (8) or as controls (8) (Figure 2).

Vegetation and fuels

In each experimental unit, 3 vegetation plots (0.02 ha each) were located by mapping their positions in a pre-set triangular pattern (Figure 2) and then placing them on the ground using a hand-held Global Positioning System (GPS) device. In each plot, crown base height was estimated on all trees with a diameter at breast height (DBH, approximately 1.37 m) greater than 5 cm. Trees below 1.37 m in height (seedlings) were sampled in two 3m by 3m subplots, with only species and frequency noted. One-year seedlings that could not be identified were excluded from the analysis. Canopy closure was measured at the northwest corner of each plot using a spherical densiometer.

Dead and down fuels were measured according to conventional methods: five points were selected in each experimental unit according to a pre-set mapped pattern (Figure 2), located on the ground using a GPS. From each starting point, two 20 m long transects were directed towards pre-determined azimuths, for a total of 200 m of line transect per experimental unit. The two transects were ensured to be more than 90 degrees apart and to never cross other transects or vegetation plots.

Woody fuels were measured along these transects according to the protocol of Brown's (1974) line-intersect method, with the addition of litter and duff depth measurements at three points along each transect. On each transect, woody fuels below 0.635 cm in diameter (1 hr time-lag) were counted for a length of 2 m; fuels between 0.635 cm and 2.54 cm (10 hr) were counted for 3 m; fuels between 2.54 cm and 7.62 cm (100 hr) were counted for 5 m; and fuels above 7.62 cm (1000 hr and above) were counted for the entire transect length. Calculations were made using values for Pacific Northwest mixed-conifer forests derived by van Wagtendonk et al. (1996). Litter and duff weights were calculated using regression equations from Agee (1973).

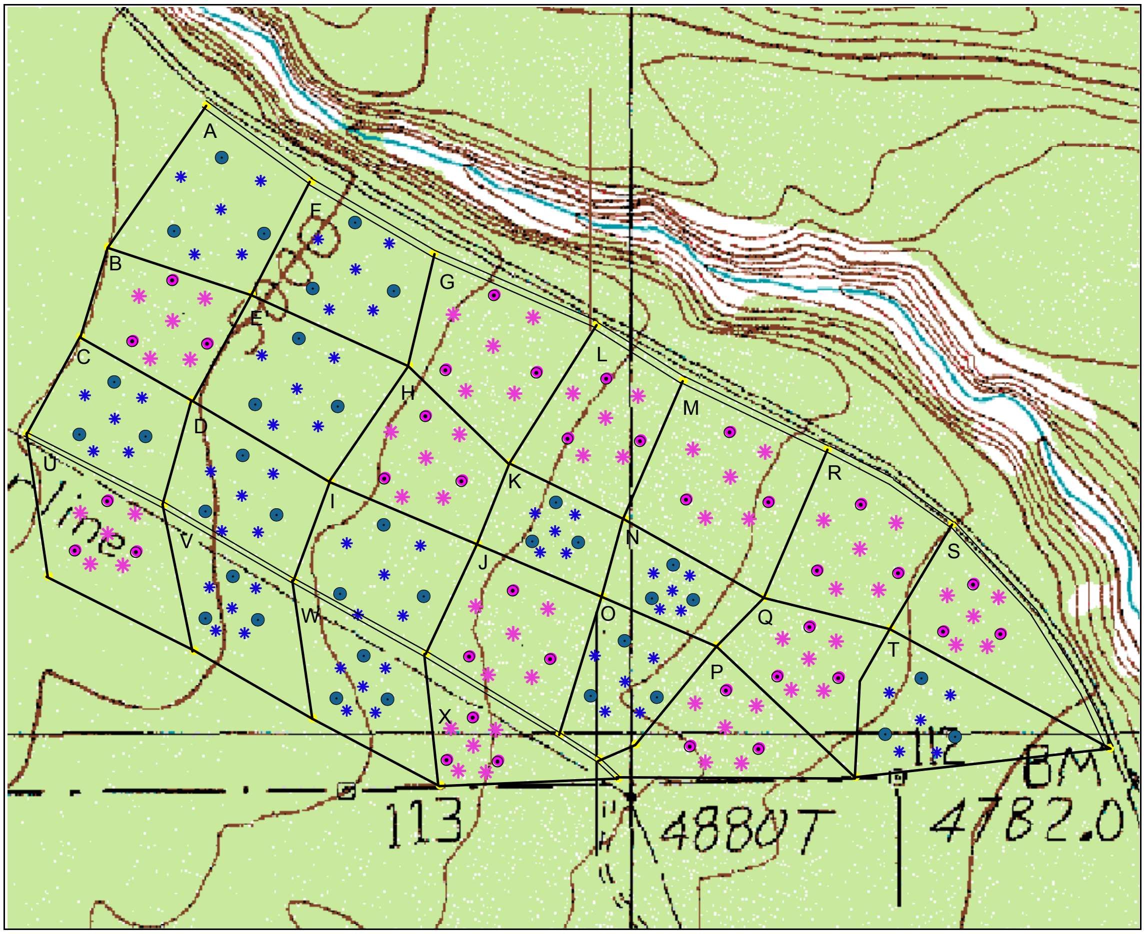


Figure 2. Study area design, including locations of fuel transects (asterisks) and vegetation plots (circles). Blocks A, C, E, K, O, T, V, and W are spring burns (blue); blocks B, H, J, L, M, Q, R, and X are fall burns (pink); and blocks D, F, G, I, N, P, S, and U are controls (for resin monitoring, D, F, I, and N are associated with spring burns, and G, P, S, and U are associated with fall burns).

Ponderosa pine mortality and resin monitoring

Within each experimental unit, all large (dbh>20 cm) ponderosa pines (PIPO) were located, tagged and had their dbh measured. In addition, all ponderosas were assessed for crown vigor according to Keen's (1943) crown classes of A (full, vigorous crown) through D (sparsely foliated, denuded and declining crown). A subset of these were then selected for resin monitoring: in each unit, two class "A" (high vigor) and two class "C" (low vigor) ponderosas were randomly selected among those present for a total of 96 trees. Where there were no class "A" trees in an experimental unit, class "B" trees were selected instead.

Out of these 4 trees per unit, one tree of each crown vigor class (two per unit) was also subjected to a light raking around its base. This treatment consisted of scraping away litter and downed wood using hand rakes from the vicinity of each tree's bole, especially from the raised "apron" (mostly bark litter) surrounding these trees for 1-2 meters. Occasionally, chainsaws were used to remove large downed logs abutting tree boles, although other live trees rooted in this zone were left intact. The duff, identified by the presence of mycorrhizal hyphae and fine roots, was undisturbed as much as was possible. Raked fuel and debris were then scattered outside the tree's drip line, taking care not to disturb any nearby fuel transects or vegetation plots. Following burning (in spring and fall burn units), the percentage of the ground fuel that had been consumed in each apron was visually estimated in order to evaluate the effectiveness of burning in altering fire behavior in the trees' immediate vicinity.

Resin flow (OEF) and pressure (OEP) measurements

Recent studies examining conifer resistance to bark beetles have mostly measured resin yield at the cambial surface. A popular method (e.g. Santoro et al. 2001; Feeney et al. 1998) was initially devised by Lorio (1993), whereby discs of bark and phloem are removed from the bole using an arch punch, while the exuding resin is channeled into vials for collection. While this method is effective for extracting resin, it has the disadvantage of causing fairly large wounds to sample trees; as a result it may be inappropriate for taking multiple measurements on one sample, or in studies where tree survival is strongly desired (such as when measuring old-growth trees in protected areas). Furthermore, such wounds are quite difficult to close, and can be expected to release resin volatiles into the air continuously until the resin crystallizes, potentially attracting insects and pathogens, such as turpentine beetles (Erbilgin and Raffa 2000; Hobson et al. 1993). A less damaging method was sought for this study, as multiple measurements were needed on each tree and the trees themselves were large old-growth specimens inside a federally protected area.

Resin flow (OEF) was measured according to the following procedure, a method combining aspects from both Lorio (1993) and Cobb et al. (1968): two 5.159 mm (13/64”) diameter holes were drilled at breast height (~1.37m) on approximately opposite sides of the bole. Holes were drilled at an angle, approx. 30 degrees below horizontal, each to a depth of about 2.5 cm into the sapwood, and redrilled several times to clean out any woody residue. Funneling “scoops” (Figure 3) made of 6.35mm (1/4”) diameter, 0.762 mm (0.030”) wall brass tubing (Alaskan Copper and Brass, Seattle, WA) were inserted into these holes to a depth not exceeding the inner edge of the bark (i.e. not into the phloem or woody tissues). Graduated cylinders (25 mL) were suspended to the ends of the funnels to collect the resin, and resin volume was noted 24 hours (± 1 hour) after drilling (Figure 4). Following resin collection, holes were plugged with small (~7 cm) sections of 6.35 mm (1/4") clean wooden dowel.

Resin pressure (OEP) was measured according to a protocol adapted from Vité (1961). Two 2.381 mm (3/32") diameter holes were drilled horizontally on approximately opposite sides of the bole, each to a depth of 2.5-3.5 cm into the sapwood. Holes were redrilled several times to clean out any woody residue. A "plunger" made of a 3.175 mm (1/8") diameter piece of steel rod was tapped into each hole after drilling to expand it slightly before inserting the nipple. Pressure gauges were Ashcroft Duralife models (Dresser Instruments, Stratford, CT) calibrated from 0 to 200 pounds per square inch (0-1379 kPa; Figure 3). Nipples were made of 10.5 cm lengths of 3.175 mm (1/8") outside diameter, 0.813 mm (0.032") wall brass tubing (Alaskan Copper and Brass, Seattle, WA) inserted and soldered to a 9.53 mm (3/8") compression fitting/bell reducer (see Figure 3). Nipples were filled with Glycerin before being attached and tightened to the pressure gauges. A small amount of adhesive caulking was applied to the outside circumference of the nipples, approximately 2.5 cm from the tip. The steel "plunger" was removed from each drilled hole immediately prior to inserting the gauge/nipple combination, which was squeezed into the hole hand-tight, until the tip of the nipple was about 5 mm from the back of the hole. Gauges were left overnight to stabilize, and OEP measurements noted the next day at 1300h (± 1 hour; Figure 4).

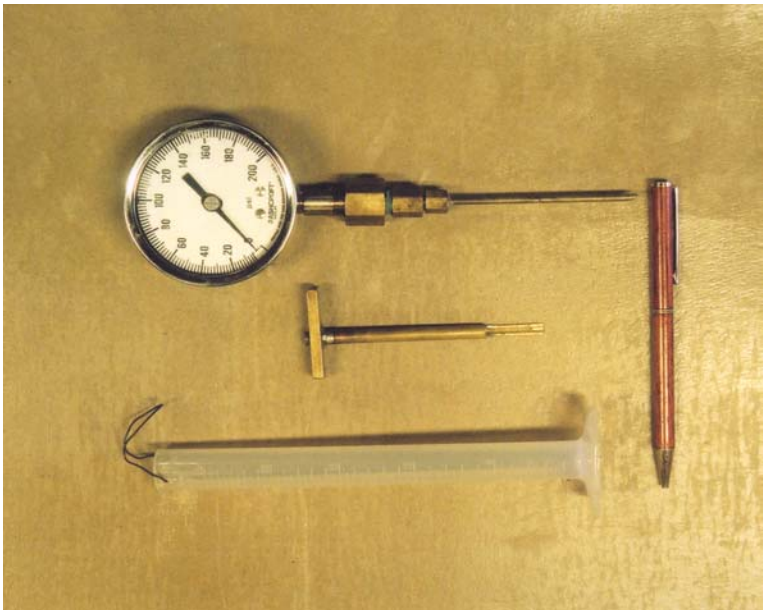


Figure 3. Resin flow and pressure equipment used in this study. From bottom to top: 25 mL cylinder, brass tube funnel, and pressure gauge (with nipple attached). Pen in photo is shown for scale.

Figure 4. OEP and OEF measurements in a pole-size ponderosa pine (not in the study area), showing ~5 mL of resin and a pressure reading of approximately 1240 kPa. Note: in this study, OEP and OEF were NOT measured simultaneously.

Oleoresin flow and pressure are dependent on many factors, including number of resin ducts, tree water relations, resin viscosity, temperature, time of day, and season (Bourdeau and Schopmeyer 1958; Vité 1961; Harper and Wyman 1936). Thus, for comparison purposes, measurements taken on different trees should ideally be taken simultaneously. However, this is often impossible, even with a modest sample size (due to constraints on equipment, labor, distance between trees, etc.); nonetheless, separate measurement "sets" should still be as close together as possible, and should be considered biased when time and/or conditions between parallel measurements are high. In this study, OEF and OEP were measured in trees on spring burns units and controls on 5 occasions over two seasons: OEF – June 6-27, 2002 (pre-burn); July 1-10, 2002; August 5-14, 2002; July 14-16, 2003; and August 19-21, 2003; OEP – June 4-25, 2002 (pre-burn); July 1-10, 2002; August 5-13, 2002; July 7-10, 2003; and August 12-15, 2003. On fall burn units, OEF and OEP were measured on 4 occasions over two seasons: OEF – September 3-12, 2002 (pre-burn); October 13-19, 2002; July 14-16, 2003; and August 19-21, 2003; OEP – September 3-12, 2002 (pre-burn); October 13-18, 2003; July 7-10, 2003; and August 12-15, 2003.

Since resin properties in spring and fall burn units were not measured at the same time the first year, control units were randomly split in half by season. Thus, 4 units were assigned as "spring controls" and 4 as "fall controls" (see Figure 2). Trees in control units in each season were measured for OEF and OEP at the same time as burn units.

Prescribed fire treatments

Burn treatments were applied in spring (June) and fall (October) 2002. Fire was applied using drip torches in a strip headfire ignition pattern (Martin 1990). In addition, to ensure that all ponderosa pines were affected by the treatment, all large ponderosas were entirely ringed with torch fuel twice along their "aprons" (1-2 m from their boles; Figure 5). Ignitions were completed in approximately 0.5-1 hr, and once fire had been applied throughout a unit, it was not reapplied, regardless of burn patchiness. During all burns, on-location weather conditions were measured every half-hour by burn personnel.

Spring burns were ignited between June 20th to 28th, and were each allowed to smolder for 7-8 days, at which point they were mopped up using water exclusively (no hand tools). Fall burns were lit on October 9th and 10th 2002. Due to fire control concerns and budget constraints, the 8 fall burns were all ignited one after the other, within a fairly short duration of time over two days. Burns were allowed to smolder until they were naturally extinguished several weeks later by rain, but most fire activity and fuel consumption took place within few (3-4) days after ignition.

To estimate the proportions of each unit that actually were affected by the fires, I counted paces along the length of two diagonal transects, approximately from one corner to its opposite in each unit. Along these transects, I noted the number of burnt ("black") and unburnt ("green") paces to give an approximate estimate of burn coverage.

Figure 5. All ponderosa pines in burn units were “ring-fired” with drip torch fuel twice during ignition to ensure that they were affected by burn treatments (Photo: Jennifer Hooke).

Data analysis

Treatment effects on fuel weights were modeled according to the multiplicative model $post = f(pre \times treatment)$,where *post* represents fuel weight after treatment, *pre* represents fuel weight before treatment, and *treatment* is a dummy variable denoting treatment type (spring burning, fall burning, or no burning (control)). This can also be expressed as a log-linear model: $\ln post = \beta_0 + a \ln pre + treatment$, where *a* and β_0 are fitted constants (β_0 is the model intercept, following statistical convention). A multiplicative model was fitted based on the assumption that the relationship between fuel consumption and pre-burn available fuel will depend on the treatment (i.e. the season of burn, or control) as well as pre-burn fuel weight (Thomas and Agee 1986; Harrington 1981) and that the effect of pre-burn fuels may be non-linear with respect to the response. The magnitudes of mean fuel weight reduction (Mg/ha) were also compared between treatments using one-way (fixed-factor) analysis of variance (ANOVA), followed by Student-Newman-Keuls (SNK) multiple comparison tests where means were significantly different. This second, simpler method of analysis allows comparison of the absolute reduction in fuel weight between the three treatments independent of pre-burn conditions. This test was done twice: once for total measured fuel weights and differences, and once considering only the fine fuels components (1 hr, 10 hr woody fuels, and litter weight).

Forest structure was analyzed by comparing changes in crown base height (CBH) and canopy closure measurements after treatment, using one-way ANOVA and SNK multiple comparisons. Canopy closure values, being proportions, were subjected to arcsine transformation before testing (Zar 1999). Differences in CBH were subjected to the $\ln(y+1)$ transformation to stabilize sample variances (Zar 1999).

Population characteristics of the ponderosa pines in the study area were assessed using descriptive statistics. Mortality was modeled using logistic regression, an appropriate model when the response variable (survival or death of individual trees) is binary (Neter et al. 1996). The fixed-effects model took the form

$$\ln\frac{p}{1-p} = \beta_0 + \beta_1 \cdot DBH + \beta_2 \cdot Crown + \beta_3 \cdot Trt$$

with diameter at breast height (*DBH*), Keen's (1943) crown class (*Crown*), and treatment (*Trt*, spring or fall burning, or controls) as predictor variables, and *p* representing the probability of mortality in any given tree. In the first run, the *Crown* x *Trt* interaction term was also included in the model; in subsequent runs, any term not significant at least at the α=0.1 level (based on χ^2 likelihood-ratio tests; Neter et al. 1996) was excluded from the final model.

OEF values were assessed by comparing the total volume of resin extracted from each tree (sum of the yield of both test tubes) at the various measurement times. To assemble the model, 3-way analysis of variance/covariance was used in a completely randomized split-plot design (experimental units as the whole-plot factor) with the categorical factors *treatment* (burn vs. control), *raking* (raked vs. unraked) and *crown* (high vigor vs. low vigor crown classes) included, as well as all their interaction terms; DBH was included as a covariate. Model terms were dropped from subsequent tests if they were not significant at the α=0.1 level in the initial run. OEP was modeled in a similar manner, with the average pressure reading between both gauges used as the response variable. Again, the completely randomized split-plot design was used, with the grouping variables *treatment*, *raking* and *crown*, and DBH a covariate.

Because pine resistance to bark beetles may be dictated by certain threshold values of resin production (Smith 1975, 2000), it may be useful to evaluate resin flow in terms of absolute volume exuded by a given tree. However, genetically-determined between-tree variations in resin properties are often high (Smith 2000; Vité 1961), and therefore treatment effect can only be adequately assessed by standardizing resin flow values. Thus, OEF values are presented in terms of volumes collected at measurement time ($\frac{vol}{tree \cdot 24h}$), as well as differences from pre-treatment values ($\frac{vol_{post} - vol_{pre}}{tree \cdot 24h}$); means were compared accordingly across treatment types (burn vs. control) using one-way ANOVAs (identical to t-tests when there are only 2 samples) on resin volume or standardized resin volume.

Resin properties (both OEF and OEP) were measured at different times for spring and fall units in the first season, precluding direct comparison between season. However, since 4 control units were measured at the same time as the trees in each burn season (see Figure 2), resin response can still be compared between individual burn treatments and controls. In 2003 (the season after burning), resin measurements were taken at approximately the same time on spring units, fall units, and controls.

OEP measurements represent the state of the oleoresin at measurement time (Vité 1961; Lorio 1994), and may be an accurate indicator of water balance measures. While OEP is also likely to be subject to high between-tree variation, it is more likely to be influenced by immediate environmental conditions (mostly related to water balance deficit or surplus; Vité 1961). OEP measures, therefore, were not standardized by subtracting pre-burn values but are simply compared between treatment groups at the different times of measurement.

Ground fuel consumption around monitored trees (raked and unraked) was visually estimated as a proportion of area burnt. Comparisons between treatment groups were made using a Kruskal-Wallis rank-sum test, followed by Nemenyi multiple comparisons where differences were found significant (Zar 1999).

Results

Burn treatments and fire behavior

Spring burn treatments were characterized by generally cool fire behavior. In 2002, the study area was not completely free of snow until mid-June, resulting in high fuel moisture conditions and consequently very low intensity burns with considerable patchiness. These burns were characterized by poor coverage, often igniting properly only in the patches of fuel model 9 (long-needle pine litter; Albini 1976), and with an average coverage of only 37% of the area visibly charred (Table 1). Weather conditions at time of ignition varied between 19 degrees C, 43% relative humidity and 24 degrees C, 29% humidity. Winds were light, mostly from 0 to 3 km/h, with some gusts up to 10 km/h. At the flaming front, flame lengths in the spring burns were estimated at mostly between 18 and 60 cm, with occasional patches up to 150 cm in sun-warmed “jackpots” of dead and down fuel.

Fall burns were characterized by more intense fire behavior and much greater burn coverage than spring burns (Table 1). Weather at the time of ignition was cool, with a range from 11 degrees C, 49% relative humidity to 19 degrees C, 20% humidity. Flame lengths were mostly in the range of 30 to 90 cm, with localized patches up to 2 meters and occasional torching of larger sub-canopy trees. Burn coverage was significantly greater in fall burns than in spring burns ($t=6.876$ on arcsine-transformed percentages (Zar 1999), $p<0.0001$), with a mean burn coverage of 76% of the unit area.

Table 1. Estimated coverage of the prescribed burn treatments by unit (see Figure 2). Proportions were arcsine-transformed before analysis (2 sample t-test).

Spring Burns:		Fall Burns:	
	% charred		*% charred*
A	49	B	64
C	23	H	72
E	34	J	67
K	37	L	79
O	50	M	79
T	57	Q	85
V	29	R	79
W	19	X	86
mean:	37		76
P	<0.0001		

Vegetation structure

Following treatment, crown base height (CBH) measurements in burn plots were higher compared with control plots. After treatment, CBH had increased on average by 0.8 m in spring burn units, by 2.7 m in fall burn units, and decreased by 0.3 m in control units. Changes in CBH (log-transformed) were significantly different between spring burns, fall burns, and control units (ANOVA: F=21.202, $p<0.0001$; SNK multiple comparison significant at $\alpha=0.05$). Changes in canopy closure measurements were arcsine transformed after adding a dummy term to account for negative values. Changes (expressed in terms of percent openness) were greater in fall burn units (+2.1%) than in controls (-4.0%) or spring burn units (-2.1%) (F=5.784, p=0.010, SNK significant at α=0.05), although spring burn values were not significantly different from controls.

The immediate effects of burning on the overall vegetation community was the consumption of plants. One year after burning, fall burns especially had much-reduced understory abundances, as well as considerable reductions in numbers of small trees. Before burning, seedlings (trees with 0 DBH) in vegetation plots consisted mostly of white fir (found in 21 of 24 units) and red fir (17 units), with a very small number of lodgepole and western white pines, and no ponderosa pines. After burning, most units still retained at least some of the same seedling species in the plots, but ponderosa pine seedlings were also found in one spring burn unit and 3 fall burn units.

Fuels

Spring burns reduced total fuels by an average of 17.9 percent and fall burns reduced total fuels by an average of 51.8 percent. The measured change in fuels on control treatments resulted in an average increase of 13.9 percent (mostly from deviations in litter and duff measurements), indicating a considerable degree of error in these measurements.

The fitted coefficients of the multiplicative fuel model are as follows:

$$post = 4.400 pre^{0.7296} \cdot 0.7264^{S} \cdot 0.4026^{F},\ R^2 = 0.8676,$$

where S and F are dummy variables (0 or 1) representing spring or fall burn treatments, respectively (the default case, where both S and F are equal to 0, represents the control model). The model terms *pre*, *S* and *F* were all significantly different from 0 at the $\alpha=0.01$ level of significance, although the intercept term, equivalent to ln(4.400), or 1.4815, was not ($p=0.1933$). This model is shown in Figure 6, decoded for the 3 different treatments.

Absolute changes in fuel weights were also tested using one-way analysis of variance, both for total fuel weights and for fine fuels only (Table 2). Before treatment, neither total fuel weights nor fine fuel weights were significantly different between groups (total: $p=0.397$; fine: $p=0.829$). After treatment, total and fine fuel weight differences (post-burn minus pre-burn) were all significantly different (fine fuels: $p<0.0001$; total fuels: $p<0.0001$) between spring burns, fall burns and controls. Fall burns units had the largest fuel reductions, spring burn units had smaller reductions, and fuel increases were measured in controls (Table 2).

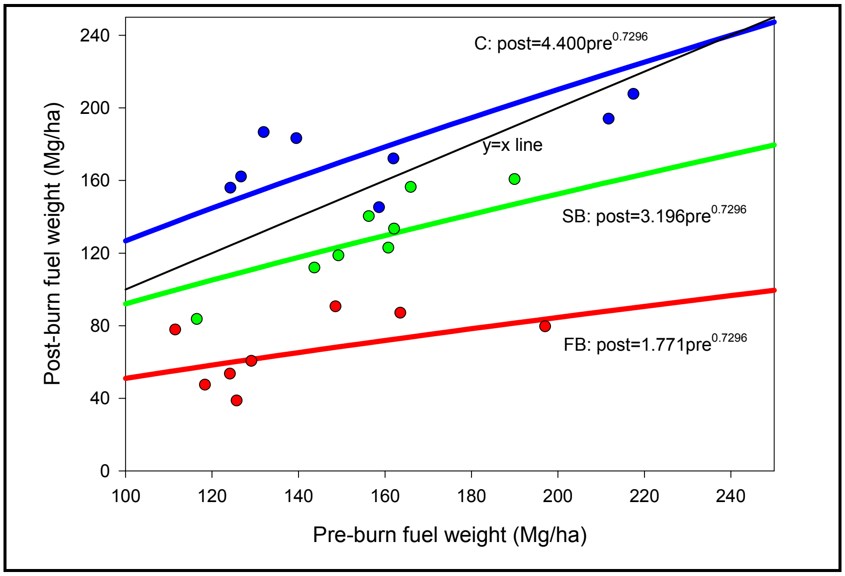


Figure 6. Total fuel model decoded for the 3 different treatments. The black line represents the theoretical control treatment (*post*=*pre*), while the colored lines represent the fitted treatment values: C – control, SB – spring burns, and FB – fall burns.

Table 2. Absolute changes in fuel weights before and after burn treatment. Pre-burn values shown represent average fuels weight of experimental units in Mg/ha ± one standard error, while post burn values represent changes in fuels from pre-burn values (*post* - *pre*) ± one standard error. Different letters following means indicate significantly different group means according to Student-Newman-Keuls multiple comparison test (α=0.05; Zar 1999).

Pre-burn	Treatment	Fuel weight (Mg/ha)	F	p
Fine fuels	Spring burn	38.5±1.643	0.19	0.829
	Fall burn	39.4±2.197		
	Control	37.6±1.985		
Total fuels	Spring burn	155.6±7.402	0.966	0.397
	Fall burn	139.7±10.120		
	Control	159.0±13.072		

Post-burn		Change in fuel weight (Mg/ha)	F	p
Fine fuels	Spring burn	-2.5a±2.897	16.152	<0.0001
	Fall burn	-11.7b±2.133		
	Control	+10.5c±3.216		
Total fuels	Spring burn	-27.0d±3.326	33.135	<0.0001
	Fall burn	-72.8e±8.441		
	Control	+16.8f±9.984		

Oleoresin flow and pressure

Due to timing constraints, it was not possible to measure OEP or OEF prior to the season of burning (2002). Pre-burn values for spring treatments were therefore collected in spring (June) 2002, in some cases only a few days before burning. In addition, these measurements were collected over a 20-day period, with data on burn units collected first, and controls collected later. For these reasons, pre-burn data on spring units is not appropriate for comparison with post-burn OEF measures (collected in mid-summer). Thus, OEF on spring units is shown as total resin flow values (in mL/24 h) with no correction for pre-burn resin flow (between-tree differences). See Discussion section for further details.

Initially, OEF was modeled as a function of burn treatment, crown class, raking treatment, and DBH. In the initial model runs, however, only the burn treatment categorical variable was consistently significant ($\alpha=0.1$). All other terms were then dropped from the model in subsequent runs.

In spring units, OEF values were different between trees in different treatment groups, with higher resin flows in control trees than in trees slated for burning (Table 3A.); because of the measurement bias noted above, however, little more can be said on the subject. Resin flows in all trees rose considerably as the summer progressed (Figure 7A). After burning, resin flows were higher on average in burnt trees than controls, although high variability in the measurements makes this observation only statistically significant one month after burning, in August 2002 ($p=0.057$). By the following July, the difference between the two group means was no longer statistically significant (July 2003: p=0.131), and even smaller yet by August (August 2003: p=0.507).

For fall burn treatments, pre-burn values were collected in summer (early September 2002) and over a much shorter time period (9 days), with no systematic bias in measurement times between treatment groups. As a result, post-burn OEF values are shown both as absolute resin-flow values (in mL), and also as changes from pre-burn values (post-burn volume minus pre-burn volume; Table 3B, Figure 7B.).

Before burning, there were no significant OEF differences between burn units and controls in fall units (Table 3B.). Immediately after burning (October 2002), resin flow was considerably lower than summer pre-burn values, but with no significant difference between burn units and controls. The following season (2003), resin flows in burnt trees were higher than control trees, both in terms of absolute resin volume (July 2003: p=0.063; August 2003: p=0.086), and especially when expressed as change from pre-burn values (July 2003 (standardized): p=0.012; August 2003 (standardized): p=0.040; See Table 3B.).

OEP measurements faced the same limitations as OEF, as well as the same bias in pre-spring burn data. In spring units, burn treatment was significant in 3 out of the 4 post-burn measurement dates at the 0.1 level. The one exception was the set of immediate post-burn measurements, which showed no significant treatment effect, but showed some correlation with DBH (p=0.081), with higher OEP proportional to larger tree diameters. In contrast, on fall units, crown class was the most commonly statistically significant factor, accounting for more variation in OEP in September 2002, October 2002 and July

2003 than other factors. Treatment was the only remotely significant factor in August 2003 in this first model (p=0.098). In July 2003, in addition to crown class, the (treatment x raking) interaction term was somewhat significant (p=0.096), as OEP was considerably higher in raked and burned trees than in trees of any other combination of raking and burning categories. DBH, as a covariate, was not statistically significant in any of the fall burn units or controls.

Following the first run, raking and DBH were dropped from the models, and the OEP data was reanalyzed including only the main effects factors burn treatment and crown class. The results from this simpler model are shown in Table 4 A and B. Burn treatment and crown class effects were both more often significant in spring units than fall units. In spring units, the most consistent pattern was higher OEP values in high vigor crown classes (Table 4A.); burned trees also had consistently higher OEP than unburned trees (Figure 8A). These effects were much less apparent in fall burns, where burning only appeared to be potentially significant (at the 0.1 level) nearly one full year after burning, in August 2003. Fall units also showed higher OEP in high vigor crown class trees, although the difference was not statistically significant immediately after burning, nor one year later, in August 2003.

Table 3 A and B. Summary of results from resin flow (OEF) data before and after burning on spring and fall treatments during the various measurement periods. Columns labeled with dates (Sep-02, Jul-03, etc.) show total resin volumes extracted from trees (mL/24 h) at one measurement time; columns labeled “diff.” represent the difference from pre-burn values (post-treatment resin volume minus pre-treatment volume). Pre-burn values on spring units are seriously biased, and are shown for completeness only (see Discussion section). Numbers in bold are significantly different at the *α=0.1 or **α=0.05 level of significance.

<u>A. Spring treatments</u>	*Pre-burn*		*Post-burn*							
	Jun-02	*St. error*	Jul-02	*St. error*	Aug-02	*St. error*	Jul-03	*St. error*	Aug-03	*St. error*
Burn units (n=8)	**1.153**	*0.490*	10.31	*1.660*	**15.69**	*1.905*	21.09	*2.423*	18.36	*2.916*
Controls (no burn; n=4)	**3.662**	*0.693*	7.23	*2.347*	**11.17**	*2.694*	12.55	*3.368*	16.02	*4.052*
p	****0.005**		0.454		***0.057**		0.131		0.507	

<u>B. Fall treatments</u>	*Pre-burn*		*Post-burn*											
	Sep-02	*St. error*	Oct-02	*St. error*	diff	*St. error*	Jul-03	*St. error*	Diff	*St. error*	Aug-03	*St. error*	diff	*St. error*
Burn units (n=8)	7.31	*1.595*	2.19	*0.773*	-5.13	*1.173*	**21.66**	*2.353*	**+14.35**	*1.797*	**25.53**	*3.051*	**+18.21**	*2.739*
Controls (no burn; n=4)	7.91	*2.255*	2.49	*1.093*	-5.42	*1.659*	**9.78**	*3.327*	**+1.88**	*2.542*	**13.94**	*4.315*	**+6.03**	*3.873*
p	0.764		0.745		0.821		***0.063**		****0.012**		***0.086**		****0.040**	

Table 4 A and B. Summary of results from resin pressure (OEP) data. Values shown are mean pressures in kilopascals (kPa). Pre-burn values on spring units are seriously biased, and are shown for completeness only (see Discussion section). Results in bold are significantly different at the *α=0.1 or **α=0.05 level of significance. Sample sizes differ between groups because of split plot design: burn treatments varied by experimental unit (N=24); crown class varied by tree (N=96). By the end of 2003, one spring-burned low-vigor tree had obviously been killed by bark beetles, and its resin pressure that year (0 kPa) is not included in the Jul-03 or Au-03 means; this explains the different standard errors for crown class for those means.

A. Spring treatments	*Pre-burn*		*Post-burn*							
Burn treatment factor:	Jun-02	*st. error*	Jul-02	*st. error*	Aug-02	*st. error*	Jul-03	*st. error*	Aug-03	*st. error*
Burn units (n=8)	79	*36.25*	310	*57.49*	**518**	*38.94*	**460**	*42.18*	**381**	*42.54*
Controls (n=4)	214	*51.26*	311	*81.30*	**356**	*55.08*	**326**	*58.60*	**236**	*59.09*
p	0.174		0.984		****0.023**		****0.048**		****0.037**	
Crown factor:										
High vigor (n=24)	135	*43.14*	**398**	*68.42*	**504**	*46.35*	**499**	*49.33*	360	*49.75*
Low vigor (n=24)	157	*43.14*	**223**	*68.42*	**371**	*46.35*	**287**	*50.17*	257	*50.60*
p	0.716		***0.071**		****0.043**		****0.002**		0.141	

B. Fall treatments	*Pre-burn*		*Post-burn*							
Burn treatment factor:	Sep-02	*st. error*	Oct-02	*st. error*			Jul-03	*st. error*	Aug-03	*st. error*
Burn units (n=8)	296	*42.53*	71	*26.31*			469	*47.71*	**327**	*39.14*
Controls (n=4)	245	*60.15*	121	*37.20*			374	*67.47*	**201**	*55.35*
p	0.533		0.271				0.251		***0.066**	
Crown factor:										
High vigor (n=24)	**368**	*50.63*	125	*31.31*			**493**	*56.78*	278	*46.59*
Low vigor (n=24)	**173**	*50.63*	68	*31.31*			**349**	*56.78*	251	*46.59*
p	****0.008**		0.194				***0.073**		0.673	

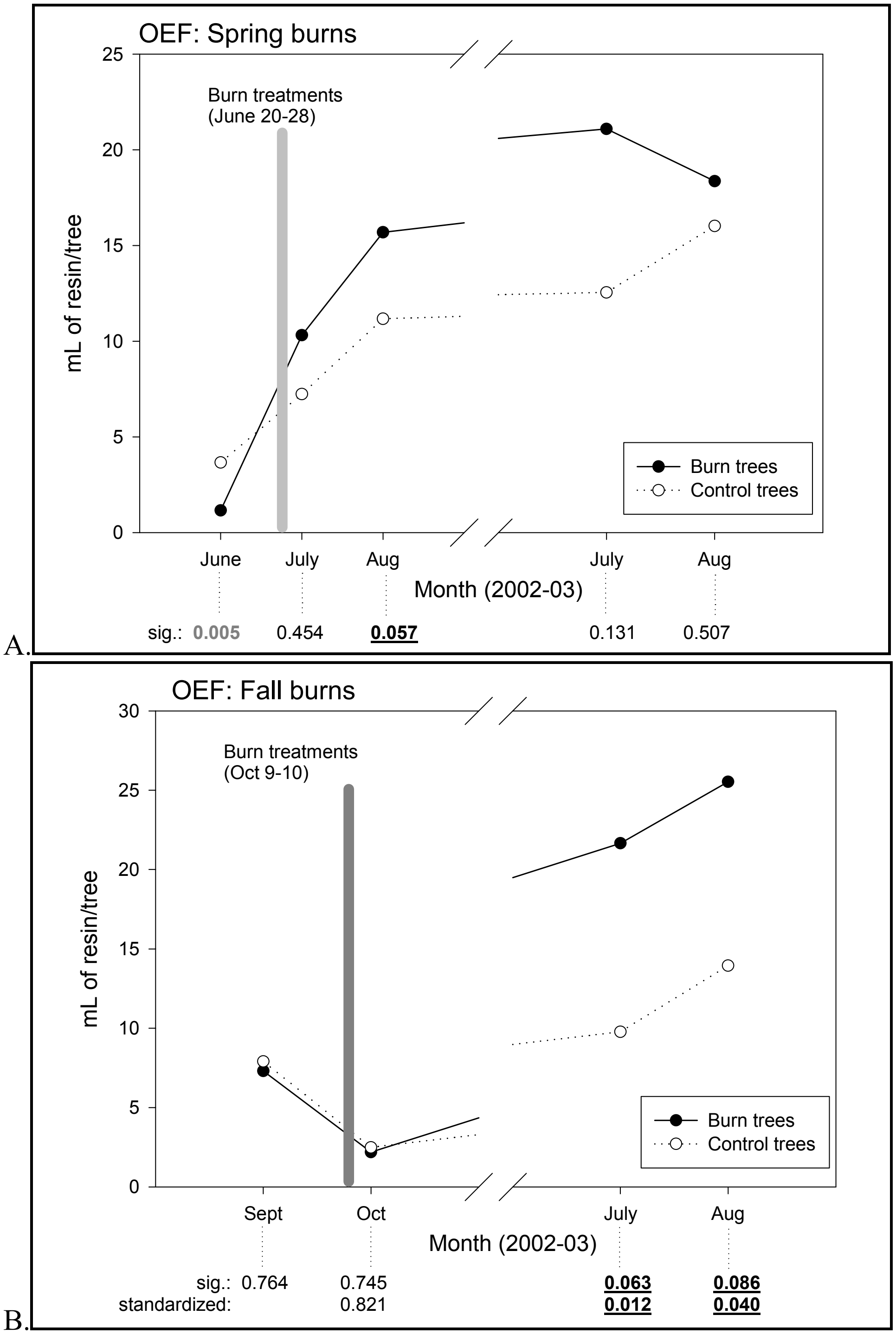


Figure 7 A and B. Summary of resin flow (OEF) data. See Table 3 for summary statistics. Underlined values are significantly different at the 0.1 level.

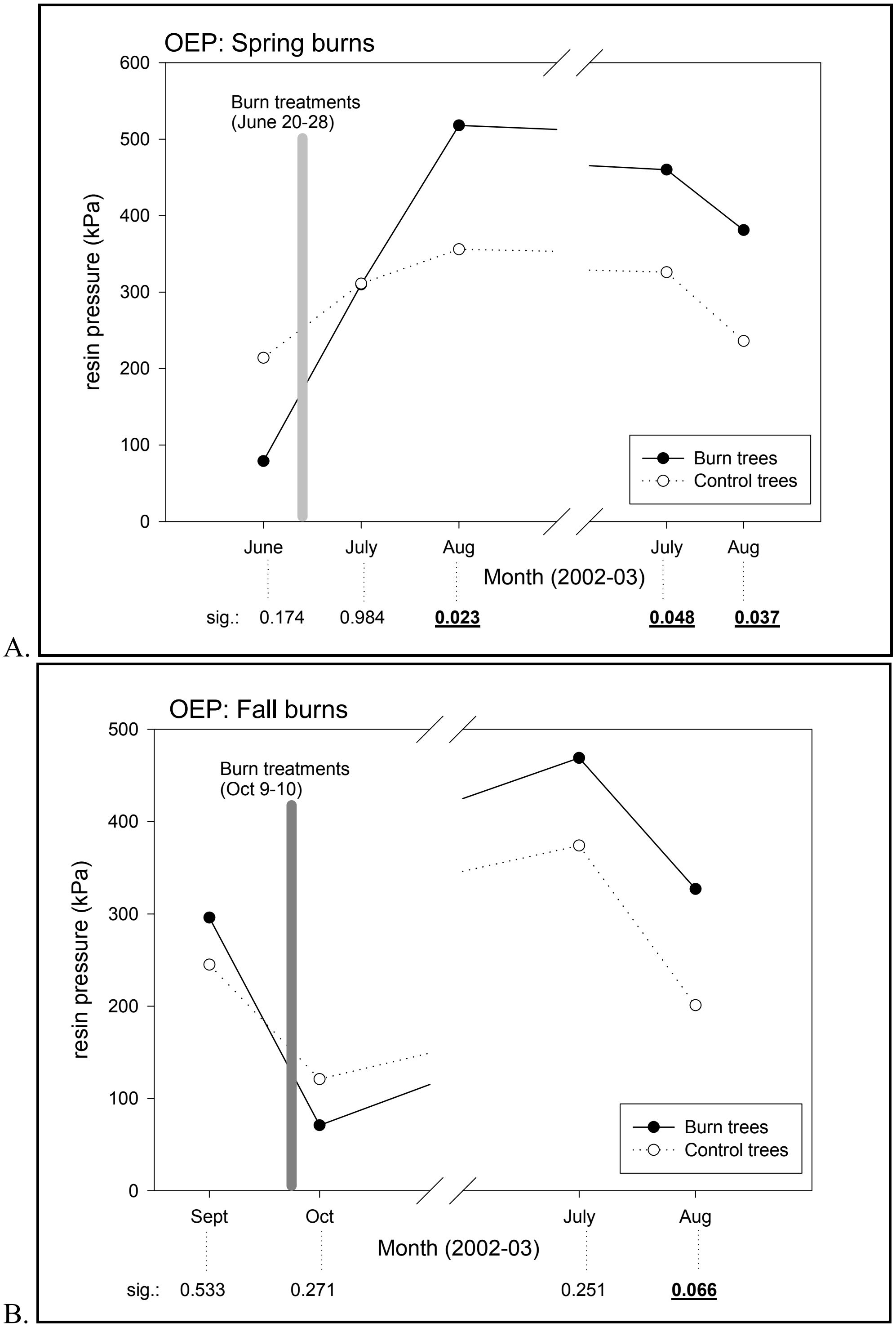


Figure 8 A and B. Summary of resin pressure (OEP) data. See Table 4 for summary statistics. Underlined values are significantly different at the 0.1 level.

Raking, burn season, and ground fuel consumption

Ponderosa pine apron fuels burned deeply once ignited. While raking may have had little discernible effect on OEP or OEF, it appeared to have had some effect on fuels and fire behavior around the bases of treated trees. Raked trees had lower percent fuel consumption around their aprons compared with unraked trees, although the difference was only statistically significant in trees subject to fall burning (Table 5). Fuel consumption appeared slightly higher in fall burns than spring burns, but means were not statistically different between seasons.

Table 5. Effect of raking on apron fuel consumption. Values shown are average estimated percentages in each category. Different letters following percentages show group means that are significantly different at the 0.05 level ($q_{0.05,\infty,4}$).

		Mean %
Spring burns:	Unraked	85ab
	Raked	73a
Fall burns:	Unraked	99b
	Raked	69a
Kruskal-Wallis χ^2		20.408
	p	0.0001

Ponderosa pine survey and post-treatment mortality

In total, 1725 ponderosa pines were identified, measured for DBH, and had their crown class noted (Figure 9A). Diameters varied between 20.4 and 179.5 cm (Figure 10), and numbers of trees as well as crown class varied considerably among the 24 experimental units. The greatest numbers of trees were in crown classes “B” and “C”, with relatively few trees in classes “A” or “D”. Before treatment, there were no ponderosa pines below 20 cm inside any units, with the exception of a very small number directly beside the highway in units M, R, and S. Ponderosa size classes were approximately normally distributed, with a mean of 94.4 cm and standard deviation of 22.4 cm (Figure 10).

One season after burning, 54 trees (3.1% of total) had died, with mortality occurring in nearly every treatment-crown class combination (Figure 9B.). Contributing factors leading to mortality appeared to be fire alone (19 trees, in burn treatment units), insects alone (5 trees, in control treatment units), a combination of burning and insects (26 trees), windthrow alone (2 trees) or after burning (2 trees), or other apparent causes (1 tree). The only samples excluded from analysis were those that were cut down for management reasons (e.g. safety concerns) during the course of the prescribed burns.

The logistic model sought to expose significant relationships between treatment, crown class, DBH, and subsequent mortality. On the first model run, only the *Treatment* and *Crown* main effects were significant at the 0.1 level, regardless of the sequence of entry into the model ($(DBH|treatment, crown): p = 0.3811$;

$(treatment \times crown|treatment, crown, DBH): p = 0.1035$)-.

The analysis was then computed a second time, including only the terms *Treatment*, *Crown*, and *Treatment* x *Crown*. All factors were significant at the 0.05 level, yielding the fitted model (1)

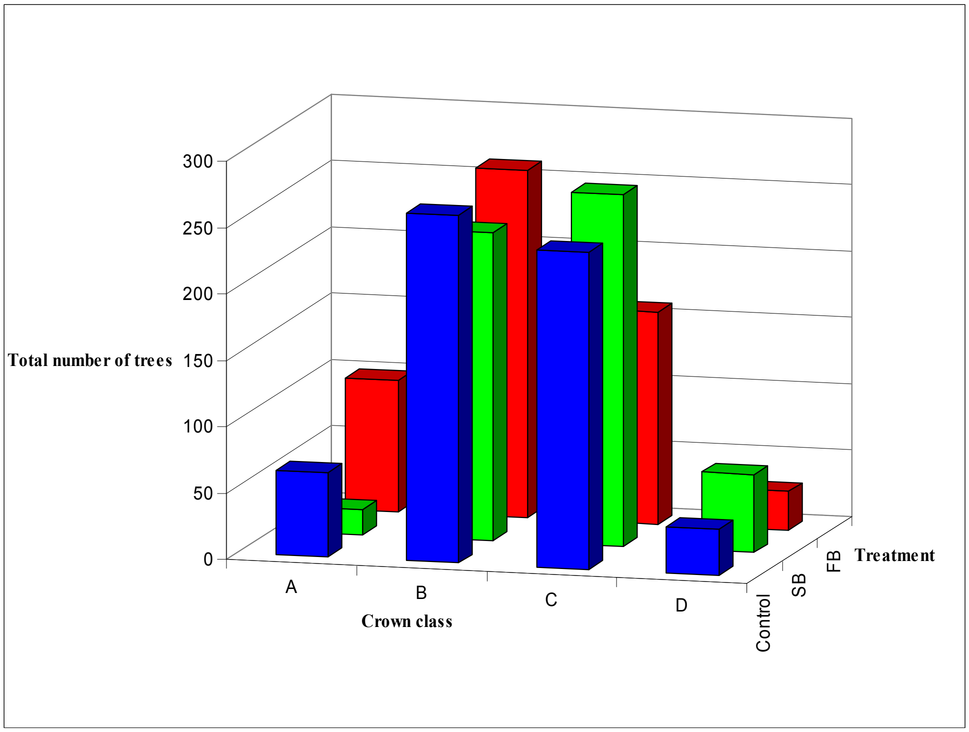
$$\ln\left(\frac{p}{1-p}\right) = -10.2 + 7.312S + 7.035F + 6.13Cr_C + 7.40Cr_D - 0.442S \times Cr_B + 0.131F \times Cr_B$$
$$- 6.85S \times Cr_C - 6.05F \times Cr_C - 7.44S \times Cr_D - 5.576F \times Cr_D.$$

(1)

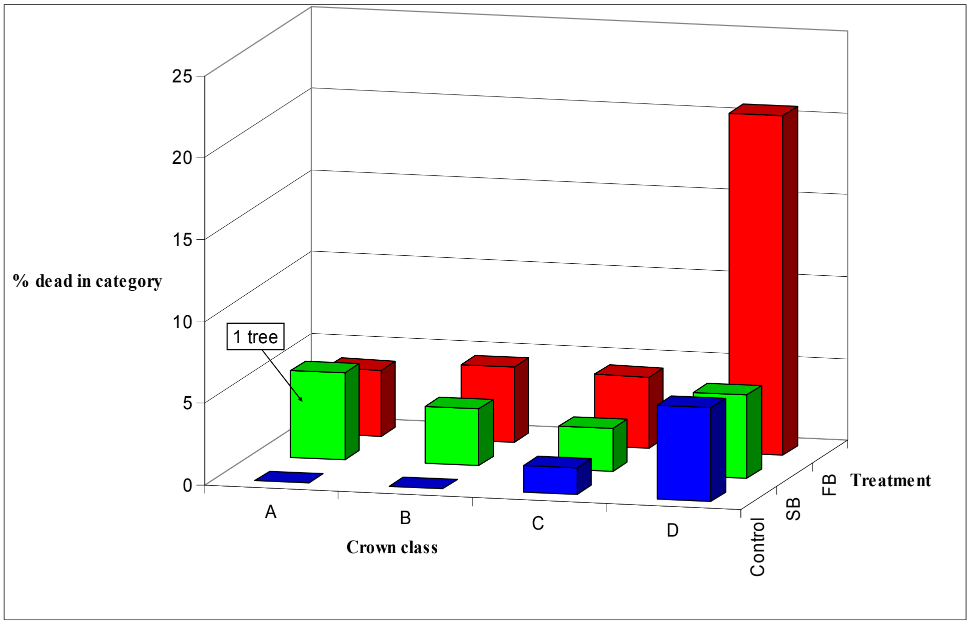
where *S* and *F* denote spring and fall burning, and the *Cr* variables denote crown classes "B" through "D" (the default case is a control treatment, and an "A" class tree). The Cr_B term was excluded from the model because its coefficient (-4.53 x 10^{-13}) was too small to be deemed significant.

Finally, the model was run only more time with only the main effects terms, *Treatment* and *Crown* included. Both terms were significant in the final model at the 0.01 level. This simple fitted model (2) is therefore

$$\ln\left(\frac{p}{1-p}\right) = -4.89 + 1.12 \cdot S + 1.75 \cdot F + 0.110 \cdot Cr_B + 0.235 \cdot Cr_C + 1.47 \cdot Cr_D \quad (2).$$



A.



B.

Figure 9 A and B. Ponderosa pine sample distribution according to crown class and burn treatment by (A) total number of trees, and (B) percent dead in each category one year after treatment. Crown class letters represent Keen's (1943) crown vigor classes. SB and FB refer to spring burning and fall burning, respectively.

Table 6 shows the matrix of predicted mortality values ($\hat{y}$ ’s, model (1)), decoded by treatment and crown class. Differences between probabilities are not necessarily significant. The model as such perfectly accounts for the number of dead trees in each crown class-treatment category, although, of course, any individual tree will have a considerable chance of survival; taken independently, the model predicts that any individual tree would survive any of the treatments, since the predicted probabilities are all below 50%.

As Table 6 and Figure 9B both show, mortality generally increased with decreasing crown vigor (increasing class code, from A to D; Keen 1943). In addition, with two small exceptions, controls suffered the lowest mortality in each category, fall burns the highest, and spring burns were intermediate. While A-class trees showed a higher percentage killed in spring burns, that sample was the smallest of any crown class-treatment combination (19 trees, 1 dead after burning), so the mortality percentage (5.3%) is not necessarily indicative of the treatment effect.

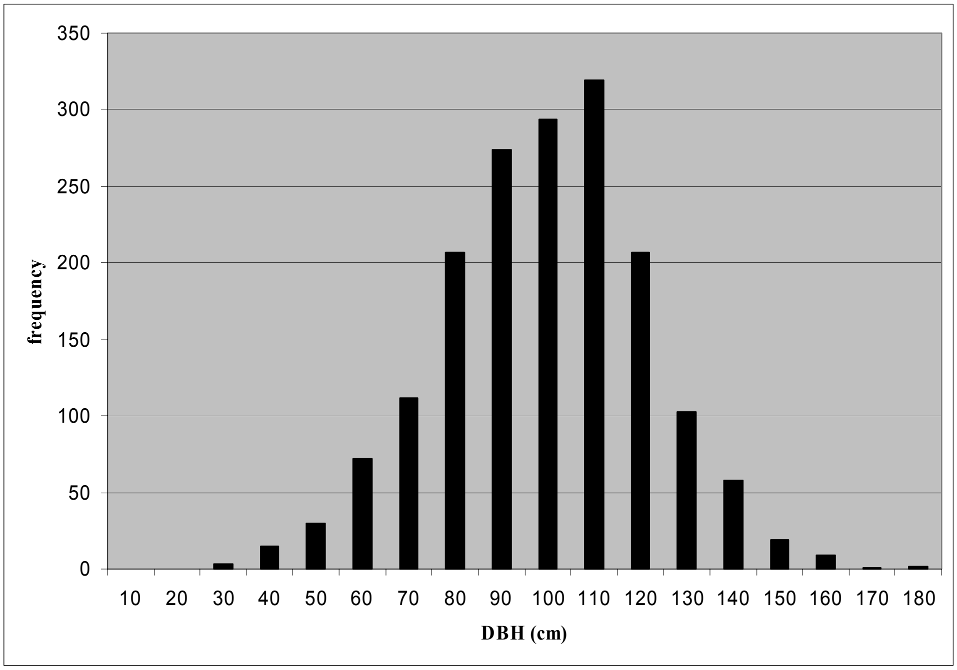


Figure 10. Size-class distribution of the ponderosa pines in the study area in all crown classes and treatment groups (n=1725).

Table 6. Predicted mortality percentages (in %) for each crown class-treatment category, as fitted by logistic regression model (1) (see text).

Crown class:	**Treatment:** Control	SB	FB
A	0.004	5.3	4.1
B	0.004	3.5	4.6
C	1.7	2.7	4.4
D	5.7	5.1	20.7

Discussion

This study attempted to analyze a number of forest parameters across a relatively small forest area. While prescribed burning research is no longer a new field, the issue of fire-bark beetle interactions remains relatively unexplored. The literature is still lacking in some fairly basic concepts regarding both the nature of these interactions and the mechanisms behind them. In this study, I attempted to address some of these mechanisms (seasonal burning effects on resin properties), while also measuring some more common fire-effects data (fuels, forest structure, etc.). The overall objective was to further the understanding of fire effects on host-tree resistance dynamics, while ensuring that the burn treatments fit in with previous management and research burns.

Burn treatments

Weather conditions during ignition of fall burns were more varied than during spring burns, even though fall burn ignition occurred over a shorter period of time. While fuel moistures were not measured, we can expect that moistures of heavy fuels varied very little over those two days (Agee 1993). During spring burns, the ten-day range between ignition times very likely caused some reduction in fuel moisture across all fuel size classes, as reflected, for the most part, in somewhat higher burn coverage during the later spring burns (units E, K, O, and T) than in the earlier burns (A, C, V, and W). The only exception to this pattern was unit A, which had relatively high burn coverage (49%)

despite being ignited earlier. As Figure 11 shows, this is probably because unit A happened to have a large open area in its interior with little fir encroachment, and consequently more sunlight and lower fuel moistures (Harrington 1981), as well as a greater proportion of the more-flammable NFFL model 9 fuel type. In general, weather conditions during the burns were well within the recommended range for fuel reduction in ponderosa pine (Harrington 1981) or sugar pine/mixed-conifer forests (Haase and Sackett 1998).

Burn coverages in this study were roughly estimated by counting paces and noting “blackened” ground; despite the low resolution of such a measure, it was clear that fire spread more actively through the fall units that those burned in spring. Criteria for burning effectiveness over large areas in other ecosystems have suggested fuel reductions on at least 50-90% or 75-80% (Fernandes and Botelho 2003) of the treated area, depending on the objectives of burning. By this measure, most spring burns in this study were not effective, although the fall burns mostly were.

Figure 11. Burn coverage in spring fires was most complete in open patches, likely due to sunlight reaching the forest floor, free air circulation, and more flammable fuels. This photo is from unit A, which had almost 50% burn coverage despite very modest fire behavior.

Fuels

Pre-burn dead fuel loads were comparable to previous studies in fire-excluded mixed-conifer forests (Thomas and Agee 1986; Haase and Sackett 1998). Reduction of fuel in both burn seasons was complicated by post-fire fuel additions. Low-intensity fires will not usually both kill and consume living trees, because of the large differences in fuel moisture between live and dead fuels (Huff et al. 1989; Agee 1993). Therefore, much of the biomass of trees killed by an initial restoration burn in a fire-excluded stand will soon become surface fuel for the next fire, whether prescribed or natural. Fuel measurements after burning in this study did not differentiate between obviously pre-existing large fuels and new additions that came about from the treatments, but it was clear that the fires created some fuels. For instance, a few of the ponderosa pines killed during the fire fell across fuel transects, resulting in large measured increases on those transects. Measured fuel reduction one year after burning will reflect the long-term treatment effect more accurately than such a measurement in the few days immediately following the burn, but does still not account for fuel additions that are certain to occur in the next few years (Thomas and Agee 1986; Agee 1993).

The regression model used pre-burn fuel weights and season of burn to predict final fuel weights. Since both treatment terms, the spring and fall burning dummy variables, were significantly different from 0 (when fitted as the final terms in the model), both spring and fall burning significantly reduced fuels compared with control treatments, where a notable increase in fuels was measured (nearly 14%). A closer examination of the data revealed that most of the difference between pre-treatment and post-treatment fuels in control units was in the litter and duff components. Assuming negligible actual increases in forest floor depth between the three seasons, this increase represents quite a large measurement error. Fuels measurements were made by different field personnel in different years, but by the same personnel in a given year. Therefore, measurement bias can be assumed to be consistent between treatments, since the same individuals measured fuels in spring units, fall units and controls within a given season. However, the nature of the litter and duff measurements – where markings on a small ruler are viewed from alongside a hole dug into the forest floor – suggest that measurement error would be much greater with increasing forest floor depths. For this reason, I believe that the measurement error on the burn units is likely to be smaller than on control units, and we should not assume that measured fuels reductions on spring and fall burn units are 14% lower than the stated values.

The average total fuel reduction measured in the fall burns (52%), as well as the increase in canopy base height (+2.68 m) suggests that this treatment was slightly more effective than the simulated treatment of Stephens (1998), a "moderate intensity, moderate consumption prescribed burn". In that study, the author found that a 50% fuel reduction following prescribed burning in previously fire-excluded mixed-conifer forest was the most effective among several stand manipulations designed to reduce potential wildfire behavior. The spring burns in our study, with an average of less than 18% fuel reduction and a very small effect on fine fuels and canopy base height, would likely be much less effective in mitigating stand-replacing fire hazard (Agee et al. 2000).

Ponderosa pine population

Overall, conclusions concerning the vegetation component of this study are premature: post-fire tree mortality can continue for several years following burning, both from the effects of the fire itself, and from insects and other pathogens. (Agee 2003b; McHugh and Kolb 2003; Swezy and Agee 1991; Thomas and Agee 1986; Harrington 1987; Agee 1993).

Figure 10 shows the profile of an aging ponderosa pine population undergoing conversion to a different forest type. Before treatment, there was no recruitment of young ponderosas to older age classes, with no seedling-size trees found in any of the vegetation plots, and virtually no trees in the entire 67 ha study area population found below 20 cm in diameter. As is the case Agee (2003a) explained for the eastern Washington Cascades, fire in ponderosa pine forests historically operated as a cyclic process, resulting in an equilibrium, rectangular-shaped age-class distribution at the forest level. Bark beetles would kill the oldest and weakest trees, and regular fires would maintain these openings and allow new seedlings to establish as single trees or small patches (Hessburg et al. 1994). The current unimodal, normal size-class distribution representing this study's ponderosa pine population contains some very large individuals for the species, but a majority of which are in declining crown vigor classes, and at serious risk of dying in large numbers. The appearance of a few seedlings after spring and (especially) fall burning, a likely consequence of creating a favorable mineral soil substrate (Schultz and Biswell 1959), suggests broader success in restoring forest health to this stressed ecosystem.

Ignoring the effects of bark beetles for the moment, the fires themselves clearly killed some large trees. Some previous studies found higher ponderosa pine mortality following growing-season burns compared with fall burns, independent of burn intensity (Swezy and Agee 1991; Harrington 1987). However, as Ganz et al. (2001) pointed out, fire intensity cannot be ignored, and intense fall burns may result in pine mortality equal to, or greater than that of a cool spring burn. In this study, the spring burns were clearly less intense than the fall burns. While the theoretically ideal experiment might involve comparing spring and fall burning under otherwise identical burning conditions, even if this could be done in this ecosystem, it would not accurately reflect the real constraints imposed by both management needs and weather (especially fuel moisture) constraints. Thus, this study observed, as did Ganz et al. (2001), considerably more intense burns in fall. One might even suggest that higher burn intensity is intrinsic to fall burning in this environment, under normal seasonal weather and management constraints.

One year after burning, we might expect that trees already killed would reflect the effects of the fire, rather than insect attacks. However, most of the mortality (31 trees out of 54, 57%) involved successful attacks of western pine beetles, with or without fire. Such a high degree of bark beetle mortality so soon after burning may bode ill for the future survival of the stand. In contrast, most of the trees that were killed in burn units without evidence of insect activity burned through near the root collar and then fell or broke during the fire (14 out of 19 trees, 74%, all but one tree in fall burn units). This suggests that fuels at the base of these trees might have led to intense fire activity near the root collar. Since the raking treatment appeared to significantly reduce fuel consumption in that region, it may be a potentially effective treatment, although slow and expensive, for mitigating against this risk.

While presence of western pine beetles was obviously the most telling sign of mortality, it is of little predictive value since the beetles are small and hard to see (Miller and Keen 1960), and it is rare to see pitch tubes or other signs indicating an unsuccessful attack; by the time a tree shows frass, woodpecker holes, or other outward signs of western pine beetles, the tree has already been killed, or will die soon thereafter (Miller and Keen 1960). Red turpentine beetles, on the other hand, leave large and visible pitch tubes outside their entry holes (Furniss and Carolin 1977), and thus can easily be counted. Within 3 years after a fairly intense fall burn in a young stand, Ganz et al. (2001) reported high pine mortality from turpentine beetles as well as from *Ips* species. Many of the trees in fall burns in this study still had green crowns (and were therefore considered alive) while showing heavy turpentine beetle activity one season after burning (including 10 trees with > 100 visible *D. valens* pitch tubes per tree). We might therefore expect considerable additional mortality among this class in the next few years, although the trees in this study are much larger than those of Ganz et al. (2001), and likely more tolerant of heavy turpentine beetle presence.

For representing immediate post-burn mortality, a significant logistic regression model was built including only the treatment and crown class terms. In this study, DBH was not a significant factor in tree mortality one year after burning, simply because of the large average size and height of nearly all the trees. This observation corresponds with previous post-fire modeling efforts in mixed-conifer ponderosa pine: Regelbrugge and Conard (1993) found the best two-variable prediction to be a combination of char height and DBH, with probability of mortality being about zero for trees above 80 cm DBH until char heights were quite high (> 20 m or so). Other ponderosa pine mortality models found crown scorch or damage estimates to be significant post-burn mortality predictors (McHugh et al. 2003; Swezy and Agee 1991; Harrington 1993). Although scorch height was not measured in this study, if any trees were significantly scorched during the course of burning, it would be in the fall burns, such as during the torching of a sub-canopy tree (Figure 12). Partly confirming this prediction, fall burns also showed the highest mortality from fire alone, although factors other than scorch height are probably also involved.

The mortality regression model in this study showed that crown class can also be important in predicting ponderosa pine mortality following burning. The combination of hot fall burning and a very low vigor (class D; Keen 1943) tree appeared particularly lethal, killing 6 of the 29 trees in this group (Figure 9B). In general, the D class trees suffered high mortality regardless of treatment, with 3 out of 59 spring burn trees and 2 out of 35 control trees having died by the end of the study. If those proportions represent a typical trend, then the area will soon be devoid of the current D class trees even without burning. At the outset of this study, there were 123 such trees in the study area; 11 have since died. If the remaining 112 are to be protected (or other similar trees in the surrounding park area), more drastic and "fine-filter" management efforts may be needed, such as mechanical thinning around individual trees, including proper off-site slash disposal, followed by burning after a delay of several years to allow trees to recover some foliage. Ponderosa pines in overly dense stands tend to suffer from low vigor and high beetle susceptibility (Sartwell and Stevens 1975; Goyer et al. 1998), so a reduction in competition should help improve health and vigor. As Smith et al. (1981) reports, trees can show improved crown class ratings (after several years) following beneficial silvicultural treatments. Kolb et al.'s (1998) findings of significantly higher resin flows (see below) 30 years after thinning in a northern Arizona stand, compared with unthinned controls, are also consistent with this premise.

Figure 12. Fall burns were clearly more intense than spring burns. This photo shows a hot spot, where a sub-canopy white fir tree has torched. The tree crowns visible in the foreground are also white firs.

Resin flow and pressure

As was suggested in previous sections, pre-burn resin data was not collected until the season of burning, resulting in data collection in mid- to late-June for spring units, a time when both OEP and OEF were very low (0 for most trees). In addition, spring unit OEF data was collected over a 20-day period during a season where resin production may have been changing rapidly (Harper and Wyman 1936; Lorio et al. 1990), and with a bias between treatment groups: resin data was collected on burn units first, and considerably later on control units. The discrepancy between collection times explains why mean OEF was significantly higher on control trees than burn trees. Furthermore, the time difference between collection of the last so-called “pre-burn” resin data (June 27th, 2002) and the first data post-burn (July 1st, 2002) is much shorter than the time between the first and last pre-burn measurements. Thus, the accuracy of the July 2002 resin data should also be considered suspect, since enough time may not have elapsed since the previous resin measures to refill the ducts (Büsgen and Münch 1929). The fact that the spring burns were mopped-up using considerable amounts of water may have also influenced this set of OEP measurements (Vité 1961); since the July 2002 spring-unit OEP values were highly non-significant between burn units and controls (p=0.984), however, that issue is somewhat irrelevant.

Ponderosa pine, unlike some other conifer species, has a highly-specialized constitutive resin system of interconnected ducts in vertical and radial directions (much fewer in a transverse direction) throughout the xylem sapwood and phloem (Bannan 1936; Phillips and Croteau 1999; Lewisohn et al. 1991). Resin is both produced and stored in the ducts (Büsgen and Münch1929) and therefore can be quickly mobilized to a wound site, such as in response to an attacking bark beetle. In addition to the quantity of resin, viscosity and crystallization are likely to play a role in the volume a tree can translocate to a particular bole or branch site, although there are conflicting reports between host tree species on whether rapid resin crystallization is associated with increased or decreased beetle resistance (Bourdeau and Schopmeyer 1958; Barbosa and Wagner 1989; Hodges et al. 1979). The exact degree of interconnectedness of resin ducts in ponderosa pine is not known, although Münch (1919; quoted in Büsgen and Münch 1929) has described ducts up to a meter in length in scots pine (*P. sylvestris*). Bannan (1936) describes the anatomy of resin canals in *Pinus* species (most work being done on *P. strobus*) as being primarily vertically oriented, scattered but wavering and non-parallel, such that two vertical ducts may overlap and connect to each other at one or more points.

In this study, OEP was measured using two pressure gauges per tree, on approximately opposite sides of the bole. Based on the known interconnectedness of resin ducts and the capacity of ponderosa pines for lateral water movement (Vité 1961), I expected pressure readings to be about equal in the two gauges at any one time, although between different measurement times there should have been high variability by time of day, weather conditions, soil moisture, season and other factors (Vité 1961). What I found was that day to day variation in resin pressure was indeed high, but also could vary tremendously between the two gauges in a single tree. The lack of correlation between the two gauge readings was such that it was not uncommon for one gauge to have a high reading (> 1000 kPa), and the other gauge in the same tree, at the same time, to be reading a value of 0. There were likely some instances of equipment and method failure, such as if the nipple opening was blocked by bark or wood chips that were not adequately cleaned out after drilling the hole. However, there were also many instances where both gauges gave definite non-zero readings but were still far apart (e.g. 700 kPa in one gauge, 150 kPa in the other). Finally, some trees steadfastly refused to show any pressure readings above 0 during the entire course of the study. Other researchers with many years of experience with these methods have also reported that zero-OEP trees were very common (D. Wood, personal communication), and that OEP data were often highly variable and frustrating to interpret (P. Lorio, personal communication). These issues appear to be more than simply operator error or inexperience.

Vité and Wood (1961) only used one gauge per tree to measure OEP, except in low-pressure trees (< 140 kPa), where two gauges were installed, and the highest of the two readings was used. In this study, the average pressure reading from both gauges was used for between-tree analyses at the various measurement times. This decision was not entirely satisfactory, given the variability described above, but seemed preferable to choosing the maximum value of the two gauges, which might overestimate overall resin pressure (and any sort of overall tree resistance which might thereby be inferred; Vité 1961), or the minimum value, which would result in a great number of zero readings – some of which would likely be due to equipment, methodology, or operator errors, rather than lack of resin pressure within the tree. Clearly, having more than 2 gauges in a tree at one time would have been preferable. Due to both the cost of additional gauges and the time required to install them, I believed that there was greater value to minimizing the time between measurements on different trees than there was to over-sampling within individual trees. In addition, there were the previously-discussed concerns regarding cumulative wounding of the sample trees, which would increase with every additional gauge installed at each measurement date.

Another further potential cause of zero-pressure readings may have been sections of dead wood in the trees. A great number of trees in the study area had some sort of scar, from past fires, insect activity, or other damage, and if the gauges were inserted accidentally into this tissue, clearly there would be no pressure reading. The fact that the trees in this study were such old (and often weakened) specimens may explain many of the problems encountered with the resin data, compared with previous studies (e.g. Vité 1961).

In any case, despite all the limitations, some statistically significant results were obtained. Unlike Vité (1961), the results from this study show that OEP generally increased during the course of the summer, reaching a peak in July or August, and dropping rapidly as temperatures cooled in October. In contrast, Vité (1961) studied younger trees at lower elevations and latitude in the Sierra Nevada, reporting highest OEP levels in January, and lowest values in July. In this study, attempts in early 2002 to collect OEP on trees while snow was still present at the site, both in mid-winter and even in late May, resulted in only zero-pressure readings. Of course, trees do not need to be resistant to beetle attacks during this time, as beetle emergence and attack times are closely related to summer temperature thresholds (Gara and Vité 1962; Peck et al. 1997). Still, the distinct difference in the seasonal OEP pattern observed in this study and that of Vité (1961) is puzzling.

Higher resin pressures were found on trees with higher vigor, in partial agreement with Vité (1961) and Vité and Wood's (1961) much-disputed (Stark 1965; Lorio 1994) original suggestion that OEP was an appropriate measure of beetle resistance. Surprisingly, following burning, OEP was also higher in burn units than in controls, with the difference being statistically significant in most post-burn measurements dates in spring units, although only at one time (August 2003) in fall units. While OEF was also higher in burn units (see below), the current belief is that OEP is a better indicator of moisture relations than of resin flow (Hodges and Lorio 1971; Lorio 1994). The water that was used to extinguish the spring burns may account for some of the increase in the 2002 post-burn OEP measurements, but cannot explain the continued difference between burn trees and controls that persisted into the following season. We are left with the possibilities that either OEP does bear some relation to OEF after all, as Vité (1961) originally believed, or for some reason burned trees had better moisture relations than controls. Since prescribed burning in this ecosystem was previously found to reduce fine root mass considerably (Swezy and Agee 1991), burning seems likely to cause moisture stress, rather than alleviate it. Wallin et al. (2003) found that prescribed fire in a young Arizona ponderosa pine stand led to increased rate of photosynthesis, and possibly improved water relations. However, the change appeared related to heavy crown scorch, which by reducing crown volume probably reduced transpiration, and thus led to increased water availability. In the present study, that mechanism does not explain the increased OEP in spring burns, since crown scorch, while not measured, was minimal in those treatments. However, in fall burns, which had much greater measured increases to canopy base height, as well as instances of observed crown scorch into the canopy of dominant trees, ponderosa pines may well have experienced some canopy reductions that led to reduced transpiration and an improvement in moisture relations. How this effect interacts with the potential loss of shallow fine roots, however is not known.

Resin flow (OEF) was somewhat more predictable than OEP, although still showed high variation between different trees and measurement sets. Individual OEF measurements were probably much less prone to errors than OEP measures from such factors as clogging, due to a larger diameter tube and simpler installation protocol than in the pressure measurements. In general, mean resin flows were higher in burn treatments than in controls, although these differences were not significant in several cases because of high sample variances. Resin flows in all treatment groups also appeared to increase throughout the summer, with peak flows in July or August, depending on the group. A separate sample of 25 young ponderosa pines in the nearby Sun Pass State Forest were monitored seven times between June and September 2003 (Perrakis, unpublished data); those trees showed the highest resin flows in mid-August, confirming this pattern.

The only spring burn measurement with potentially significantly different ($p < 0.1$) OEF sample means occurred one month after burning, in August 2002. Had we been able to properly collect pre-burn OEF in these trees and standardize the OEF measurements (as in fall burns), the change in resin flows from burning might have been more statistically significant (by reducing between-tree differences due to vigor), although that assertion is untested. In fall burns, the immediate post-burn resin flows (October 2002) were not significantly different between treatment groups, but since many of the individual trees exuded no resin at that time (0 mL), it was likely too late in the season for meaningful comparisons. Again, mid-October is probably past the dispersal time for most western pine beetles at this elevation and latitude, dispersal being strongly controlled by temperature thresholds (Miller and Keen 1960; Gara and Vité 1962).

The two most meaningful sets of resin measurements were probably the 2003 fall burn OEF measurements. Both July and August data show higher resin flows in burned units than in controls; differences in treatment means were modestly significant ($p < 0.1$), made considerably more so by standardizing to reduce between-tree variation ($p < 0.05$).

Previous studies have previously reported increased resin flows in conifers following various types of injury. While wounding does not appear to cause an immediate increase in resin flow in ponderosa pine, as it does in other conifers such as *Abies* (Lewisohn et al. 1991), induced short-term (< 1 week) resinosis has been found in loblolly pine (*P. taeda*; Ruel et al. 1998). Laboratory experiments on other *Pinus* species have generally reported increased resin duct formation at longer time scales, i.e. after 3 months or more, after wounding seedling-size plants (Fahn and Zamski 1970; Bannan 1936). Distance of wounding effects on resin duct formation ranged from about 12 cm in Aleppo pine (*P. halepensis*; Fahn and Zamski 1970) to up to several meters in Scots pine (*P. sylvestris*; Büsgen and Münch 1929) from the injury location, depending on the degree and type of wounding, and probably on species. Bannan (1936) also suggested that increased resin duct formation in Pinaceae conifer species was greatest when injury occurred during the growing season, and much lower when it occurred in dormant periods; it is not clear, however, what species were observed before making that assertion.

In a field setting, variations in resin response have also been seen following various types of stand manipulations. Working on loblolly pine, both Nebeker and Hodges (1983) and Fredericksen et al. (1995) observed increases in resin flows that persisted for 2-3 months after applying various mechanical injury treatments to study trees. In the latter study (Fredericksen et al. 1995), however, resin flows were significantly reduced the following season on stressed trees compared with controls. Unfortunately, fewer studies of the sort have been done on ponderosa pine. Kolb et al. (1998) noted that 30 years after various thinning treatments in a second-growth ponderosa pine forest, OEF was much higher (although highly variable) in thinned trees than in unthinned controls, and that resin flow appeared negatively correlated with stand basal area. Similarly, Mason (1971), measuring initial resin flow rate through capillary tubes in young loblolly pine, noted higher resin flow rates in thinned trees (one year after treatment) compared with unthinned controls. However, Feeney et al. (1998) noted no significant increase in resin flow one year after thinning in old-growth ponderosa pine in Arizona. In the second year of study, significant increases in OEF occurred in trees subjected to thinning and a low-intensity prescribed burn, as well as significantly higher flows on all trees (Feeney et al. 1998). It may be important to note that that burn in that study was not reported to cause any crown scorch to the study trees. In contrast, Wallin et al. (2003) measured significantly lower resin flow in heavily scorched trees compared with less-affected trees, a few months after a moderate-intensity broadcast burn in a young ponderosa pine stand.

Based on all of this previous research, it appears that resin flow in ponderosa pine is a factor both of overall tree vigor as well as recent injury, although it may take more than a few days for resin production to respond, and more time yet before the impact of increased resin production can be measured through the commonly-used technique of draining resin canals in select bole locations. Resin flow is already difficult to measure, and the fact that current measurement techniques impose further physical injury on study trees presents a major confounding factor that has not been often addressed. Crown scorch in such fires may additionally complicate the response, by reducing carbon intake capacity and carbohydrate production (Mooney 1972), but also causing reduced transpiration and an improvement in water relations.

Thus, the fact that resin flow in this study increased one season after fall burning is not overly surprising. The increase was likely a factor of additional resin duct formation brought about by cambial injury (Bannan 1936; Ryan 2000), although growth-differentiation principles (Lorio et al. 1990; Herms and Mattson 1992) may also be related. Observed increases in bark beetle attack success following prescribed fire – the original premise behind this investigation – were often delayed by 3-7 years (Agee 2003b); thus, seeing increased resin flow, and presumed higher bark beetle resistance, one year after burning is not inconsistent with that observation. In future years, however, I expect that resin flows in burnt trees will decline: moisture stress from fine root mortality should lead to stomatal closure (Hsiao 1973) and reduced gas exchange, lowering carbohydrate production (Mooney 1972) and availability for resin production.

Several studies measuring pine resin flow repeatedly in the same trees, including this one, have observed higher resin flows during the course of their experiments, in controls as well as treatment trees (e.g. Feeney et al. 1998; Fredericksen et al. 1995; Nebeker and Hodges 1983). While this variation has usually been attributed to weather patterns and soil moisture (e.g. Feeney et al. 1998), little attention has been granted to the injury effects of the resin sampling methods. If Bannan's (1936) and Münch's (1919; quoted in Büsgen and Münch 1929) findings on laboratory seedlings so many years ago also apply to adult trees, then even modest physical injuries to tree stems can cause some degree of increased resin duct formation, and repeated resin measurements in individual trees are very likely to show heightened resin flows during the course of the experiment, regardless of additional treatments that might be the primary focus of such studies. Mason (1971) briefly mentions this issue; many more recent studies do not. Finally, I suggest a certain caution in interpreting the results of these older studies: while the authors often claim to speak for the entire *Pinus* genus (e.g. Bannan 1936), most testing was done on one or two species, with *P. sylvestris* being a popular choice. Their generalizations may apply in whole, only partly, or not at all, to *P. ponderosa* or other species.

When we add the still-unconfirmed effects of growth-differentiation tradeoffs (Lorio 1990; Herms and Mattson 1992), weather variations from season to season, and sometimes over several seasons (e.g. Agee 2003b), and the intrinsic difficulties of studying bark beetles – organisms who spend most of their life cycle hidden from view, and respond most strongly to their own pheromones (Wood 1982), it is perhaps not surprising that confusion should still exist regarding the dynamic relationship between bark beetles and their hosts under varying conditions, as well as what methods are best for measuring and capturing the desired interaction effects. The addition of the vagaries and stochasticity of fire into this equation adds considerably to an already profound challenge. It is my opinion that the lack of modern attention to this research topic at the tissue or cellular level is severely limiting our understanding of fire-bark beetle dynamics. Addressing this paucity of ecophysiological data would help greatly in explaining some of the inconsistencies which exist within this area of inquiry.

Thus, both OEF and OEP measurements were higher in burned trees than in controls after prescribed fire. Differences were not always significant, but the opposite pattern, reduced resin defenses in burned trees, was certainly not observed one year after burning. When we combine these observations with the observed increases in beetle-related mortality in trees subject to burning, we arrive at perhaps the most surprising finding of this study: a positive correlation between resin defenses and beetle activity. Explaining this pattern may require us to abandon some previously-held beliefs. If OEP or OEF do indeed indicate resin defenses, as several studies suggest they should (e.g. Smith 1975, 2000; Hodges et al. 1979; Vité and Wood 1961), then primary attraction may be occurring after all. While Moeck et al. (1981) found no evidence of primary attraction of western pine beetles to ponderosa pine (neither cut wood samples nor weakened trees), their experiments did not examine the possible effects of fire. Further research examining the role of fire in initiating primary attraction would help answer this question, although such studies would be difficult to design in a manner that would allow conclusive results. In the meantime, further monitoring of the trees in this study should help show if at least long-term post-fire beetle-caused mortality can be explained by a delayed reduction in host defenses. In the short term, however, there is no evidence for such a mechanism.

Management considerations

Assuming similar weather at burn time, the main differences in fire intensity between spring and fall burns is fuel moisture. In a system such as southern Oregon mixed-conifer forest, with wet, snowy winters and summer droughts, and poor soil moisture retention (Youngberg and Dyrness 1964), spring consists of a short season of rapid drying, while fall can be a long or short period of increasing moisture. Therefore, if fire is to be applied in spring, the most likely fuel component to burn will be the recently dried out fine fuels. In contrast, in autumn, with the approximately opposite weather trend occurring, heavy fuels (large logs) are more likely to be consumed (e.g. Thomas 1982). This difference has important implications for prescribed fire. Where objectives of burning include reducing total fuel weights, the bulk of which consist of heavy wood and duff (Agee 1993), fall burning will likely be more effective. If a prescription calls for reducing fine fuels while leaving heavier fuels intact (such as for wildlife habitat purposes), then spring burning may be effective for such purposes, at least in theory. In practice, reducing total fuels is a far more common management objective (Walstad et al. 1990; Agee 1993), and for the most part, it appears that fall burning will be more effective for such purposes in mixed-conifer forest.

One additional serious complication related to spring burning is a resource availability issue: by the time the snowpack has disappeared from mountainous areas (such as the study area) and spring burning becomes possible, other western forests (e.g. in the Rocky Mountains, west slopes of the Cascades, etc.) are well into their dry seasons, and fire suppression resources may be in high demand. This situation was very evident in the course of this study, when suppression crews and equipment from all across the US were being sent to Colorado to combat the (eventually) 55,000 ha Hayman fire, which began on June 9th, 2002 (Graham 2003). While this may have been an artifact of the unusually hot and dry 2002 fire season, there is much evidence that such “unusual” years are becoming more and more common (Agee 1993) – a trend related, of course, to the reasons behind prescribed burning for fuel reduction purposes in the first place! The season that is ecologically and climatologically meaningful as “Spring”, at Crater Lake, corresponds to early summer in much of the US, and it will likely be continuously difficult to gather sufficient personnel and permissions to accomplish spring burns under these conditions. By the time the autumn burning season arrives, the situation is very different, as dropping temperatures and increasing precipitation across much of the country vastly reduce the number of new ignitions, while helping extinguish the few large fires still burning from the summer.

An additional problem relates to “mop-up”, or the extinguishing of prescribed burns once they have been lit. Following spring burns, there will be great pressures on fire managers to extinguish the burns soon after ignition, to avoid having burns actively occurring during the hotter and drier weather that will surely arrive within days (Mike Powell, 2002 Crater Lake interim Burn Boss, personal communication), at least in Pacific Northwest forests. As a result, much of the benefits of the burn, in terms of fuel reductions and fire effects, may be lost (depending on the treatment objectives) if mop-up is done shortly after ignition on a low-intensity burn. In the case of fall burns, cooler temperatures and precipitation are much more likely to arrive in the days weeks soon after burning, allowing for the possibility of a “natural out”, requiring no mop-up, and allowing for greater fuel consumption during the a lengthy smoldering period. Both conditions occurred during the burns in this study, and explain to a large extent the reason why the spring burns had such low burn coverage.

Conclusion

This study sought to compare the effects of prescribed burning in spring and fall on a number of variables in mixed-conifer/ponderosa pine forests. Overall, the spring burns appeared only marginally effective at meeting the burn objectives of fuel reduction and forest health restoration. However, few of the large pines were killed in spring burns, which was a primary objective of the burning treatment.

Ponderosa pine resin activity (pressure and flow) was somewhat higher in spring-burned trees than controls, although high variability in the data and numerous potentially confounding effects limit the conclusions that can be drawn from such observations. Additional resin monitoring will be required for several more years, both to test the hypothesis of correlation between long-term reductions in resin defenses and subsequent increased insect activity in these forests, as well as to help improve the accuracy and usefulness of such methods for predictive purposes.

The fall burns were considerably more intense, appearing effective at reducing fuel loads, and causing significant beneficial changes to vegetation structure. A greater number of dominant pines were killed in fall burns than in spring burns or controls, although the numbers were still quite low. However, both injury to the ponderosa pine population as well as post-burn insect activity appeared to be higher in fall-burned trees, suggesting potential increases in tree mortality following these treatments in the years to come. Ponderosa pine resin properties in fall burns responded more or less similarly to spring burns, although with more significant resin flows in the season after burning. These increases were believed to be mostly caused by the trees' physiological response to injury. Combining the findings of observed increases in bark beetle activity in burned trees with a lack of reduction in measured resin defenses leads to the tentative conclusion that primary attraction may be occurring following fire, although further studies are needed on this subject.

Overall, there was little question that the fall burns were more successful at meeting the treatment objectives in this study, and burning in fall seems more appropriate for future restoration treatments in this ecosystem than burning in spring. However, overly intense fires, which are more likely in fall burns, should be avoided in order to prevent losses to an already-stressed old-growth pine population. Managers must seek the delicate line representing the ideal burning conditions for restoring the ecosystem without destroying it in the process. This represents a challenging goal, one which prescribed burning alone may not be capable of meeting.

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