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Delayed conifer mortality after fuel reduction treatments: interactive effects of fuel, fire intensity, and bark beetles

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Abstract. Many low-elevation dry forests of the western United States contain more small trees and fewer large trees, more down woody debris, and less diverse and vigorous understory plant communities compared to conditions under historical fire regimes. These altered structural conditions may contribute to increased probability of unnaturally severe wildfires, susceptibility to uncharacteristic insect outbreaks, and drought-related mortality. Broad-scale fuel reduction and restoration treatments are proposed to promote stand development on trajectories toward more sustainable structures. Little research to date, however, has quantified the effects of these treatments on the ecosystem, especially delayed and latent tree mortality resulting directly or indirectly from treatments. In this paper, we explore complex hypotheses relating to the cascade of effects that influence ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) mortality using structural equation modeling (SEM). We used annual census and plot data through six growing seasons after thinning and four growing seasons after burning from a replicated, operational-scale, completely randomized experiment conducted in northeastern Oregon, USA, as part of the national Fire and Fire Surrogate study. Treatments included thin, burn, thin followed by burn (thin + burn), and control. Burn and thin + burn treatments increased the proportion of dead trees while the proportion of dead trees declined or remained constant in thin and control units, although the density of dead trees was essentially unchanged with treatment. Most of the new mortality (96%) occurred within two years of treatment and was attributed to bark beetles. Bark beetle-caused tree mortality, while low overall, was greatest in thin + burn treatments. SEM results indicate that the probability of mortality of large-diameter ponderosa pine from bark beetles and wood borers was directly related to surface fire severity and bole charring, which in turn depended on fire intensity, which was greater in units where thinning increased large woody fuels. These results have implications when deciding among management options for restoring ecosystem health in similar ponderosa pine and Douglas-fir forests.

Key words: burning; Douglas-fir; latent mortality; path models; ponderosa pine; restoration treatments; stand structure; structural equation modeling; thinning.

Introduction

Pre-Euro-American low-elevation dry conifer forests of the western United States were shaped by frequent low- or mixed-severity disturbances such as wildfires (Agee 1993, Taylor and Skinner 1998, Everett et al. 2000, Ottmar and Sandberg 2001, Wright and Agee 2004, Youngblood et al. 2004, Hessburg et al. 2005, Arabas et al. 2006) and insect attacks (McCullough et al. 1998, Hayes and Daterman 2001) mediated by diverse environmental gradients of topography, soils, and weather. The challenge that now faces ecologists and resource managers is to integrate knowledge of these same disturbances or their potential surrogates to better understand how these various agents determine forest structure and composition. Surface fires, ignited predominantly by lightning during the time of year when moisture content of fine fuels was lowest (Agee 1993, Rorig and Ferguson 1999), controlled regeneration of fire-intolerant species, reduced density of small-diameter stems, consumed litter and down wood, opened the stands to increased sunlight, led to vertical stratification of fuels by eliminating fuel ladders between the forest floor and the overstory canopy, and maintained relatively stable plant associations. Consequently, the structure of these low-elevation dry forests generally consisted of open, park-like, with widely spaced individual or small clumps of medium to large, typically uneven-aged live trees, scattered dead trees, and low herbaceous understory vegetation (White 1985, Wick-

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man 1992, Agee 1994, Kaufmann et al. 2000, Wright and Agee 2004, Youngblood et al. 2004, Arabas et al. 2006, Brown and Cook 2006).

Insects are major components of forest ecosystems, representing much of the biological diversity and affecting virtually all processes and functions. In the United States, bark beetles (Coleoptera: Curculionidae, Scolytinae) heavily influence the structure and function of conifer ecosystems by regulating primary production, nutrient cycling, ecological succession and the size, distribution, and abundance of forest trees (Fettig et al. 2007). While we know little about abundance of arthropods and their interspecific relationships in pre-Euro-American conifer forests (Short and Negrón 2003), low-elevation dry conifer forests supported many indigenous phytophagous insect species that killed trees, especially phloem-boring bark beetles and cambium and wood boring beetles (Coleoptera: Buprestidae and Cerambycidae) (de Groot and Turgeon 1998, McCullough et al. 1998). Attacks often led to mortality of individual and small groups of trees, created snags, altered the accumulation of fuels and vegetation, and created canopy gaps that provided opportunities for new seedling cohorts (Hessburg et al. 1994, Hayes and Daterman 2001).

Today, many low-elevation dry conifer forests have characteristics that place them at greater risk of severe wildfire compared to pre-Euro-American forests under natural disturbance regimes. These features include greater mass of down woody debris and continuity of fuels at landscape scales, more small trees and fewer large trees, greater proportion of young multi-storied forests containing fire-intolerant conifers in both understory and overstory strata, and more frequent fuel ladders that contribute to greater flame lengths during fires (Agee 1993, Covington and Moore 1994, Arno et al. 1997, Taylor and Skinner 1998, Harrod et al. 1999, Youngblood et al. 2004, 2006, Hessburg et al. 2005, Stephens and Gill 2005). In low-elevation dry forests of the Pacific Northwest, altered fuel beds and shifts in forest structure and composition have resulted from fire exclusion and suppression, livestock grazing, timber harvests, and changes in climate (Bergoffen 1976, Steele et al. 1986, Dolph et al. 1995, Arno et al. 1997). Increases in overall stand density over the past century have led to increased competition among trees for below-ground nutrients, water, and growing space, thereby increasing their susceptibility to bark beetles and other forest insects and diseases (Mitchell 1990, Hessburg et al. 1994, Oliver 1995, Fettig et al. 2007).

In the past two decades, unusually large and catastrophic wildfires across the western United States have heightened public awareness of forest ecosystems and raised concern for forest health. There is broad agreement that some form of fuel reduction treatment is necessary to move stands from their current structure and developmental trajectory to conditions that are healthier, more resilient to fire, and may incorporate natural disturbance regimes prevalent under pre-Euro-American influences (Starr et al. 2001, Allen et al. 2002, Brown et al. 2004, Graham et al. 2004). Recent presidential initiatives such as the National Fire Plan, the 10-year Comprehensive Strategy, and the Healthy Forests Initiative, and legislation such as the Healthy Forests Restoration Act of 2003 (P.L. 108-148), have promoted the consideration of large scale and strategically located fuel reduction and restoration projects to manage landscapes within the context of ecological processes (U.S. Department of the Interior and U.S. Department of Agriculture 2006). These fuel reduction and restoration treatments often are applied in low-elevation dry conifer forests as thinning or prescribed burning projects, and are designed to reduce surface fuels, to decrease crown density while retaining large live and dead trees of fire resistant species, to increase the height to the live crown, and to promote late seral structures, with the goal of reducing the risk of uncharacteristically severe surface and crown fires (Brown et al. 2004, Agee and Skinner 2005).

There is increasing recognition that both fire and insects are critical and intrinsic components of low-elevation dry conifer forest ecosystems because they both affect species composition, nutrient cycling, stand dynamics and development, and can have consequences for forest productivity and biological diversity (Preisler and Mitchell 1993, Agee 1998, de Groot and Turgeon 1998, McCullough et al. 1998). Yet land managers implementing fuel reduction and restoration treatments often lack an understanding of how these treatments affect fire and insects as agents of natural disturbances (Fiedler et al. 1992, Pollet and Omi 2002, Noss et al. 2006, Pilliod et al. 2006). Although many studies of disturbances in low-elevation dry conifer forests have focused on fire or insect outbreaks as independent events, these disturbance agents are often causally related. By creating snags, causing needles to dry and drop prematurely, changing fuel continuity and thus determining the nature and rate of fuel decomposition, bark beetles change the composition, quantity, size, distribution, compactness, and arrangement of forest fuels. These factors influence the initiation, intensity, and spread of wildfires at various temporal scales. In addition, fires in low-elevation dry conifer forests predispose surviving trees to attack by insects. Some species of wood borers are attracted to fires, smoke, and fire-injured trees and they find and select ovipositing sites in freshly burned wood before competitors arrive (Wickman 1964, Evans 1971, McCullough et al. 1998). Trees that rely on oleoresin exudation as a primary defense to bark beetle and wood borer attack must shift resources to address wounding caused by the fire. Thus, trees with crowns scorched or boles charred by fire are weakened and are less resistant to insect attack (Fellin 1980, de Groot and Turgeon 1998, McCullough et al. 1998, Parker et al. 2006, Fettig et al. 2007).

Fuel reduction and forest restoration treatments such as thinning and prescribed burning may have both direct and indirect effects on residual trees, and these effects may lead to tree mortality. There is no clear understanding of the network of direct and indirect causes of tree mortality and especially the processes that contribute to postfire mortality of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) (Fowler and Sieg 2004). One analytical approach for addressing such complex ecological interactions and multiple controlling factors is structural equation modeling (SEM) (Grace 2006). SEM is a multi-equational framework for evaluating complex hypotheses about multiple causal pathways among networks of variables. In this paper, we use SEM to investigate tree mortality in response to multiple factors after fuel reduction and forest restoration treatments.

This work is part of the Fire and Fire Surrogate (FFS) study (Weatherspoon 2000, McIver et al. 2008), a national network of 12 long-term study sites established to evaluate the ecological consequences of treatments for reducing fuels and restoring forest ecosystems. The effects of thinning and prescribed burning treatments on vegetation, fuels, wildfire hazard, soils, wildlife habitat and use, insect population dynamics, and ecosystem structure and processes are being evaluated in 12 fire-dependent ecosystems. Details of the network and links to individual sites are available at the study web site (*available online*).[5]

Here we report on work from one FFS study site that addresses latent or delayed conifer mortality and the effects of insect attacks after fuel reduction treatments. We relate tree mortality to changes in stand structure (Youngblood et al. 2006) and fuel beds (Youngblood et al. 2008) one and four to six years after treatments in low-elevation dry ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) forests in northeastern Oregon. We address the hypothesis that manipulative treatments such as thinning and prescribed burning create distinctly different stand structures in the short-term ($<$5 years posttreatment) when compared to non-manipulated or control treatments, and these changes in structure create conditions that affect insect response. The following specific objectives are addressed in this paper: (1) characterize bark beetle and wood borer population dynamics as a result of fuel reduction and restoration treatments; (2) identify the factors influencing posttreatment mortality of ponderosa pine and Douglas-fir after fuel reduction and restoration treatments; (3) relate this information to ecological restoration of ponderosa pine and Douglas-fir in low-elevation dry forests of the Pacific Northwest.

Methods

Study area

This study was conducted in the northern Blue Mountains of northeastern Oregon, USA. The study area (45°40′ N, 117°13′ W; 1040 to 1480 m elevation) includes almost 9400 ha of plateaus, benches, and deeply incised drainages formed in highly fractured ancient Columbia River basalt. Forest composition and structure in the study area are representative of warm and dry biophysical environments common throughout the upper Columbia Basin of Washington and Oregon. The climate is strongly continental; mean annual temperature is 7.4°C at the closest weather station in Enterprise, Oregon (45°42′ N, 117°5′ W; 1000 m elevation) with continuous records since 1969. Frost can occur any month of the year. Mean annual snowfall is 66 cm and mean annual precipitation is nearly 500 mm at Enterprise, but slightly higher at the study area. Moisture within the growing season results from highly variable convection storms.

Recent human-caused disturbances, especially past timber cutting, grazing practices, and exclusion of wildfire have left stands of mainly 70- to 100-year-old even-aged ponderosa pine and Douglas-fir that regenerated after extensive partial cutting. Overtopping this cohort is a stratum of remnant and scattered large and old trees left during previous harvest entries. At least two harvest entries within the past several decades reduced tree densities in some stands. During the early 1990s, the study area was affected by elevated levels of bark beetles, especially mountain pine beetle, *Dendroctonus ponderosae*, and pine engraver, *Ips pini*. Understory vegetation composition is dominated by relatively few species of shrubs and graminoids (Youngblood et al. 2006). Plant associations (Johnson and Simon 1987) represent a majority of the variation in dry forests of the Blue Mountains.

Treatment implementation

Experimental units ranged from 10 to 20 ha, and were randomly selected from a population of stands with similar topographic features and stand structure for an operational experiment with a completely randomized design consisting of four treatments replicated four times. Treatments included: (1) thin, (2) burn, (3) thin + burn, and (4) control. Active treatments (thin, burn, and thin + burn) were designed to reduce the total basal area from about 26 to about 16 m^2/ha and reduce surface fuel mass in the 0–7.62 cm (1–100-h time lag) classes to $\leq$4.5 Mg/ha. Detailed descriptions of treatment implementation are available elsewhere (Youngblood et al. 2006, 2008).

The thinning treatment was a single entry low thin (removing trees from the lower crown classes to favor those in the upper crown classes) favoring ponderosa pine for retention over other species. Trees were cut by using a cut-to-length harvesting system featuring a single-grip harvester and forwarder to remove merchantable live trees and standing dead and down material. Forwarders used the same trail system as the harvesters, operating on top of the accumulated limbs and tree tops within trails that ran up or down slope

[5] ⟨http://frames.nbii.gov/ffs⟩

TABLE 1. Environmental setting and initial stand conditions of experimental units across four fuel reduction treatments in northeastern Oregon, USA.

Unit	Treatments	Size (ha)	Elevation (m)	Aspect (degrees)	Slope (%)	No. plots	Live density (trees/ha)	Live basal area (m^2/ha)	Plant association†
245	Control	13.8	1286	218	11	21	452	14.4	*Pinus ponderosa/Symphoricarpos albus*
15	Control	15.1	1113	108	18	10	425	29.4	*Pseudotsuga menziesii/Calamagrostis rubescens*
18	Control	7.5	1333	296	26	19	567	19.7	*Pseudotsuga menziesii/Calamagrostis rubescens*
23	Control	12.0	1379	345	10	28	432	17.7	*Pseudotsuga menziesii/Calamagrostis rubescens*
8B	Burn	10.1	1170	82	8	23	287	17.1	*Pinus ponderosa/Festuca idahoensis*
10B	Burn	8.4	1920	50	8	21	219	12.4	*Pinus ponderosa/Festuca idahoensis*
21	Burn	10.4	1373	230	18	30	265	19.4	*Pseudotsuga menziesii/Calamagrostis rubescens*
24	Burn	8.4	1260	84	9	23	374	12.8	*Pinus ponderosa/Festuca idahoensis*
6A	Thin	14.4	1361	283	11	26	827	24.7	*Pseudotsuga menziesii/Calamagrostis rubescens*
7	Thin	11.9	1305	292	21	25	868	30.4	*Pseudotsuga menziesii/Symphoricarpos albus*
9	Thin	9.1	1235	51	12	23	711	15.5	*Pinus ponderosa/Agropyron spicatum*
22	Thin	8.8	1380	286	8	28	386	17.2	*Pseudotsuga menziesii/Spirea betulifolia*
6B	Thin + burn	12.1	1388	221	15	29	695	19.3	*Pseudotsuga menziesii/Calamagrostis rubescens*
8A	Thin + burn	10.4	1174	297	9	23	285	18.3	*Pinus ponderosa/Festuca idahoensis*
10A	Thin + burn	15.9	1186	297	13	24	330	12.3	*Pinus ponderosa/Festuca idahoensis*
1112	Thin + burn	11.0	1185	274	9	27	282	15.6	*Pinus ponderosa/Festuca idahoensis*

† A relatively stable plant community of definite composition growing in a uniform habitat; see Johnson and Simon (1987).

within each unit. All thinning occurred between July and October 1998. Individual burn plans were developed for experimental units to account for differences in site physical features and fuel accumulations. Burn plans predicted direct mortality from fire of <30% for ponderosa pine between 20 and 51 cm diameter at breast height (1.37 m) (dbh), and <20% for ponderosa pine ≥51 cm dbh. Burns were conducted in mid-September 2000 under conditions conducive to low flame heights (<1.8 m). Experimental units to which the thin + burn treatment was assigned were thinned in 1998 and then burned in 2000.

Field methods

We characterized temporal changes in levels of tree mortality in ponderosa pine and Douglas-fir by assessing bark beetle and wood borer presence before and after treatment and attributing tree mortality to specific insect presence. Before treatments were applied, a systematic grid of sample points was established along compass lines within each unit, with sample points 50 m apart and ≥50 m from stand boundaries. A total of 380 sample points was established within the 16 experimental units, permanently marked, and geo-referenced by GPS (Table 1). Circular 0.04-ha plots were centered on each grid point, and all standing trees ≥1.37 m in height were inventoried by species, noted as live or dead, and their height measured to the nearest 0.1 m using a telescoping height pole or clinometer. Diameter of each tree was measured at 1.37 m above the ground with a diameter tape. Individual trees were assessed for visible indicators of bark beetle attack, such as fading or changing needle color, boring dust, location and color of pitch tubes, and woodpecker activity along the bole. Trees with any external indicator of bark beetle attack were numbered and tagged. Trees judged dead, based on complete lack of green foliage, were examined by removing portions of the bark on the lower bole to reveal the inner bark and sapwood. Species of bark beetle was determined by pitch tube shape and location, pattern, and characteristics of galleries. Pretreatment inventory was conducted in 1998, and posttreatment tree inventories were conducted in 2001 and in 2004, the sixth growing season after the thin treatment and the fourth growing season after the burn treatment.

Many bark beetle species attack trees in non-uniform spatial patterns, resulting in small group kills (e.g., <10 trees) or patches of trees up to a few hectares in size. To guard against undetected bark beetle activity, we augmented assessment for bark beetle presence in circular plots by conducting unit-wide assessments in 2002 and 2003. These were conducted as a 100% census of all trees with any external indicator of bark beetle attack or tree mortality. When bark beetle attacks were noted, the probable bark beetle species was recorded, tree species and tree diameter were recorded, trees were referenced by distance and compass bearing to the closest grid point, and were numbered and tagged.

The western pine beetle, *Dendroctonus brevicomis*, feeds exclusively on ponderosa pine in our study area, while the mountain pine beetle and the red turpentine beetle, *D. valens*, attack all pines in the study area and will sometimes attack Douglas-fir. The pine engraver also attacks pines while the Douglas-fir beetle, *D. pseudotsugae*, and the Douglas-fir engraver, *Scolytus unispinosus*, are monophagous on Douglas-fir. Flatheaded borers (Buprestidae) and roundheaded borers (Cerambycidae) are difficult to distinguish to species. Individual trees often are hosts to multiple species of bark beetles and wood borers. The precise contribution of each insect species to tree mortality can be difficult to detect. Therefore, we ranked the bark beetle species in terms of effectiveness as a tree killer a priori based on published literature (Furniss and Carolin 1977) and local knowledge. We considered western pine beetle to be the most effective in killing ponderosa pine because it makes winding galleries that girdle portions of the bole, is capable of multivoltine cycles, and has a propensity for attacking fire-injured pines. Other bark beetles in decreasing effectiveness were mountain pine beetle, pine engraver, any of the wood borers, and finally red turpentine beetle. Likewise, the ranking for bark beetles found in Douglas-fir was Douglas-fir beetle, Douglas-fir engraver, and any wood borers. Thus, any ponderosa pine with a combination of galleries and pitch tubes indicating western pine beetle, mountain pine beetle, and red turpentine beetle had mortality attributed to western pine beetle.

Causal agents that might mediate the effects of treatments on tree mortality included measures of fire severity (both tree charring and surface fire severity), physical damage (tree bole damage), fire intensity, and fuel mass (both ground and surface fuels). Tree charring is defined as the frequency of trees with bole char, which is uniform charcoal-like bark damaged during the passing fire front observed on each tree. Surface fire severity was represented by the amount of mineral soil exposed, defined as the percentage of the surface area of the plot lacking organic cover, and was estimated ocularly within the grid-point plot. Physical damage was the result of damage from mechanical harvesting equipment on residual tree bole, defined as the removal of bark and exposure or destruction of cambium. The maximum vertical and horizontal dimensions of scars on the lower 2 m of bole were measured to the nearest cm. Bole char, surface severity, and physical damage were sampled before treatment in all units, after all treatments except in controls in 2001, and again in all units in 2004.

As a surrogate of fire intensity, we used recorded fire temperature. Pyrometers (ceramic tiles with 25 different temperature-sensitive lacquer spots) (Omega Engineering, Inc., Stamford, Connecticut, USA) were staked 2 m directly south of the center of each grid-point plot at 0.3 and 1.2 m above the forest floor in burn and thin + burn units. These tiles provided a measure of the maximum instantaneous temperature during the passage of the flaming front within the constraints of the 25 different lacquer spots, although they provided no indication of duration. Work with similar tile pyrometers indicated that this method may underestimate maximum temperatures relative to those recorded by thermocouple, yet is sufficiently precise and accurate for characterizing fire behavior (Iverson et al. 2004, Kennard et al. 2005). Heat sensitivities of the lacquer spots ranged from 40° to 900°C with about 20°C intervals between 40° and 400°C and 75°C intervals >400°C. When individual tiles indicated no change from ambient, we assumed a uniform 23°C temperature. Fire temperature was defined as the average of the maximum instantaneous temperature recorded at both heights above the forest floor.

Fuels were sampled before treatment in all units, after all treatments except in controls in 2001, and again in all units in 2004. For the thin + burn treatment, fuels were resampled in 1999, after the thinning yet before burning. Ground and surface fuels were sampled with three transects at each of the 380 sample points using the planar intercept method (Brown 1974). The direction of the first transect at each sample point was based on a random bearing and the second and third transects were 120° on either side. The same transects (i.e., the same starting and ending points) were used for all pretreatment and posttreatment sampling. One hundred-hour fuels (2.54–7.62 cm in diameter) and 1000-hour fuels (7.62–22.86 cm in diameter) were sampled along the entire 20-m transect.

Univariate analyses

Counts of live and dead trees by unit were summarized to obtain overall percentage of dead trees in 1998, 2001, and 2004. Treatment differences among these measures of stand structure were evaluated with univariate analysis of variance (ANOVA) in a completely randomized model with Statistix version 8 software (Statistix Analytical Software, Tallahassee, Florida, USA). Assumptions of normality were tested with the Shapiro-Wilk normality test and normal probability plots (Quinn and Keough 2002). An angular transformation ($\sin^{-1}\sqrt{y}$) of these values for percentage of dead was conducted before the ANOVA. Untransformed values are presented in graphic format to aid in interpretation. Fine structure differences among treatments were examined by using planned contrasts within the context of the ANOVA. The five contrasts were specified as (1) the difference between the control and the three active treatments; (2) the difference between the mean of the thin and the burn treatments and the single thin + burn treatment (thus assessing the interaction effect of the combined treatments); (3) the difference between the thin treatment and the burn treatment; (4) the difference between the burn treatment and the thin + burn treatment; and (5) the difference between the thin treatment and thin + burn treatment. P values for each contrast were obtained as part of a univariate ANOVA and are reported when the overall F test was significant. Because these five contrasts were planned a priori, we used the least significant difference method. We set the significance level for controlling the family-wise Type I error rate to $\alpha = 0.05$.

Overall density of dead trees was computed by tree species to describe the population structure of standing dead trees in each treatment unit in 1998, 2001, and 2004. Minor amounts of grand fir (*Abies grandis*),

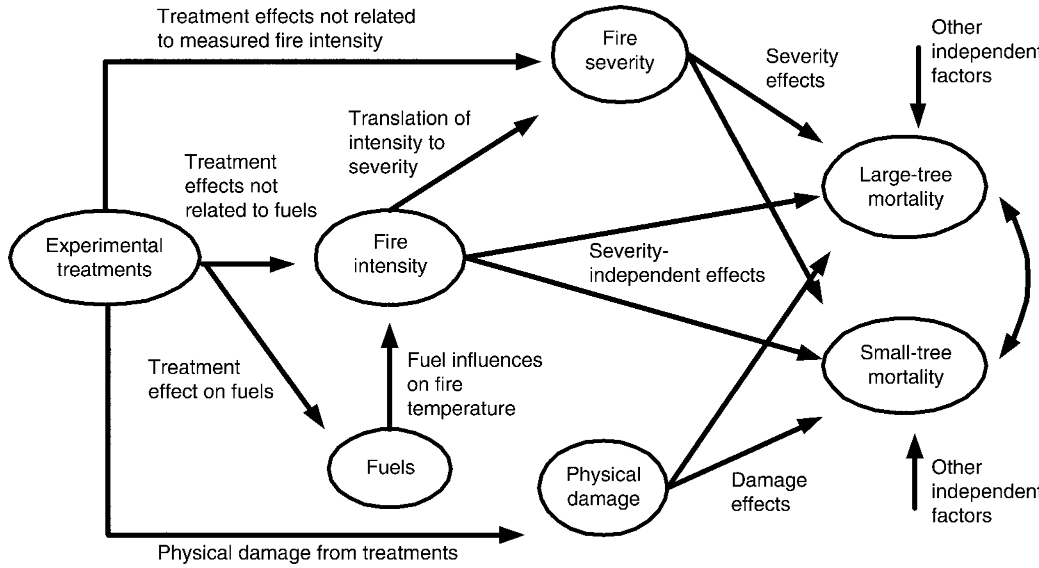

FIG. 1. Conceptual model representing hypothesized relationships among factors contributing to delayed conifer mortality after burning.

lodgepole pine (*Pinus contorta*), and western larch (*Larix occidentalis*) were combined as "other" species. A logarithmic transformation was used to normalize values before ANOVA but untransformed values are presented in tabular format to aid in interpretation. Density of dead trees also was computed by six diameter size classes to give size-frequency distributions for each unit: (1) seedlings were $<$1.37 m in height, (2) trees from 0.1–9.9 cm dbh, (3) 10.0–24.9 cm dbh, (4) 25.0–39.9 cm dbh, (5) 40.0–54.9 cm dbh, and (6) $\geq$55 cm dbh.

New mortality (posttreatment) was assessed by causal agent for 2001–2004. Mortality that occurred with no other visible indicator of a causal agent in units in which fire was applied was attributed to the fire. We used these density values to calculate a percentage of mortality based on total number of trees in each experimental unit. We based the total density of trees (both live and dead) in 2002 and 2003 on density of trees in 2001. This provided annual rates of mortality resulting from each causal agent. These data, particularly those associated with bark beetle-caused mortality, ranged from 0.0% to 4.7% and were highly nonnormal, with wide variation among replicate units in calculated percent mortality. In addition, the sample size for some species of bark beetles was very small. For these reasons, we interpreted tree mortality as a binary process and conducted a frequency distribution analysis to characterize the factors influencing probability of tree mortality. Fisher's exact test (Zar 1984) was used to evaluate the association between mortality events and treatment effects for each causal agent, including fire, wind, western pine beetle, mountain pine beetle, pine engraver beetle, red turpentine beetle, and wood borer. We collapsed diameter size classes into small trees ($\leq$24.9 dbh) and large trees ($\geq$25.0 cm dbh). These analyses were performed by using SAS version 8.02 software (SAS Institute, Cary, North Carolina, USA) and were based on the total mortality that occurred in sample plots over the course of the study that could be attributed to a causal agent.

Structural equation modeling

From the univariate analyses we concluded that bark beetle response to fuel treatments was intimately tied to fire, and that the vast majority of tree mortality occurred in ponderosa pine. Thus, we focused our investigation of causal relations of posttreatment mortality of ponderosa pine on treatments that included burning. Structural equation modeling (SEM) (Pugesek et al. 2003, Grace 2006) has been used to disentangle intercorrelated influences for a variety of situations (Grace and Keeley 2006, Harrison et al. 2006, Keeley and McGinnis 2006, Laughlin and Grace 2006).

Our SEM analysis was guided by a conceptual model that described our understanding of the relations by which forest structural conditions affected by treatments might in turn influence tree mortality in the burn and thin + burn units (Fig. 1). The hypotheses represented in this model are based on what we believe to be a plausible set of relations that include (1) fuel beds, especially woody fuels, may be influenced by different kinds of fuel reduction treatments; (2) fire intensity, the rate of heat release along the flaming front, may be influenced by the kinds and amounts of fuels present and their accumulation or removal by treatments; (3) fire severity, the degree to which a site has been physically altered by fire, may be influenced by fire intensity and other unmeasured effects not related to fire intensity, such as residence time; (4) physical damage to trees may be influenced by treatments; (5) mortality of large trees may be influenced by fire severity, fire intensity, physical damage, and

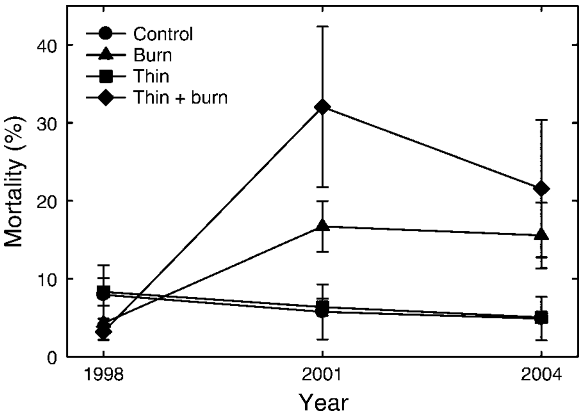

FIG. 2. Unit-level mortality (percentage of all standing trees; mean ± SE) associated with four fuel-reduction treatments in northeastern Oregon, USA.

other factors to the same degree as small trees; and similarly (6) mortality of small trees may be selectively influenced by fire severity, fire intensity, physical damage, and other factors.

We constructed structural equation models by using a multivariate data set assembled from information collected at grid-point plots, and Mplus version 4.21 software (Muthén and Muthén, Los Angeles, California, USA). Because a number of the response variables of primary interest are categorical, in particular those involving mortality, a probit model formulation (similar in concept to a logistic model) was used for those parts of the model. In our probit model, responses are linked to a continuous probability function, and as a result, path coefficients estimate the effects of factors on the probability of mortality. Estimation of the percentage of explained deviance permits a pseudo-R^2 to be calculated for the categorical responses. A hierarchical model was used to account for the fact that plots were nested within units (Hox 2002). Nonlinear effects and interactions were evaluated as part of the model process according to the procedures in Grace (2006: Chapters 6 and 7).

RESULTS

Unit-level tree mortality patterns

Pretreatment (1998) percentage of tree mortality across the 16 treatment units ranged from 1.5% to 18.6%, averaged 6.0 ± 1.1% (mean ± SE), and did not differ among treatments ($P = 0.30$) (Fig. 2). Immediately after all treatments were implemented (2001), percentage of mortality was nearly 25% in one burn unit and 50% in one thin + burn unit. Differences among treatments ($P = 0.02$) reflected the application of fire. The thin + burn treatment resulted in greater percent mortality compared to the mean of the burn and thin treatments ($P = 0.01$), and the thin + burn treatment resulted in a greater percent mortality than the thin treatment ($P = 0.01$). Percent mortality in burn units was not clearly different from that in thin + burn units ($P = 0.06$). By 2004, standing dead ranged from 1.4% to 45.6% of total trees, averaged 11.8% ± 9.9%, and did not differ among treatments ($P = 0.12$). Mortality displayed in Fig. 2 represents the instantaneous mortality estimate based on standing tree density and does not reflect changes in overall density associated with treatments, such as the reduction of density through thinning.

Pretreatment density of dead ponderosa pine, including seedlings, ranged from 1.8 to 122.0 stems/ha in 1998, averaged 29.1 ± 9.0 stems/ha, and did not differ among treatments ($P = 0.440$) (Table 2). Overall pretreatment density of dead Douglas-fir was about half that of ponderosa pine (16.7 ± 9.7 stems/ha), and did not differ among treatments ($P = 0.276$). Other species such as grand fir, lodgepole pine, and western larch were present in minor amounts (0.3 ± 0.1 stems/ha) and did not differ among treatments ($P = 0.790$). Overall density of dead ponderosa pine increased slightly with treatment as measured in 2001. Density ranged from 4.5 to 94.6 stems/h[1] in 2001, averaged 34.6 ± 7.4 stems/ha, and did not differ among treatments ($P = 0.946$). Overall density of dead Douglas-fir also increased slightly with treatment. Density ranged from 0 to 143.4 stems/ha in 2001, averaged 21.2 ± 9.9 stems/ha, and did not differ among treatments ($P = 0.649$). Density of other species was unchanged at 0.3 ± 0.1 stems/ha. By 2004, the actively treated units averaged 38.3 ± 8.7 dead ponderosa pine stems ha^{-1} and the control units averaged 13.6 ± 6.4 stems/ha, although there was no overall difference among treatments ($P = 0.874$). The overall mean in 2004 was 33.6 ± 6.8 dead ponderosa pine stems/ha. Density of dead Douglas-fir was 19.5 ± 8.5 stems/ha and did not differ among treatments ($P = 0.594$). Density of other species was unchanged from prior years.

TABLE 2. Density (no./ha) of dead trees (mean ± SE) by species before and after four fuel reduction treatments in northeastern Oregon.

Treatment	Ponderosa pine	Douglas-fir	Other
1998			
Control	28.3 ± 9.0	39.0 ± 36.1	0.3 ± 0.3
Burn	11.0 ± 1.5	0.4 ± 0.4	0.0 ± 0.0
Thin	64.4 ± 29.9	22.4 ± 16.0	0.5 ± 0.4
Thin + burn	12.6 ± 4.7	5.2 ± 5.2	0.2 ± 0.2
2001			
Control	24.6 ± 7.0	39.1 ± 34.8	0.4 ± 0.4
Burn	31.4 ± 15.2	2.0 ± 1.4	0.0 ± 0.0
Thin	50.5 ± 21.8	22.2 ± 14.5	0.5 ± 0.3
Thin + burn	31.7 ± 15.3	17.7 ± 17.7	0.3 ± 0.3
2004			
Control	19.5 ± 4.7	37.1 ± 29.4	0.4 ± 0.3
Burn	38.7 ± 15.7	4.9 ± 2.8	0.1 ± 0.1
Thin	42.3 ± 18.1	19.3 ± 11.9	0.4 ± 0.2
Thin + burn	33.8 ± 15.7	16.6 ± 16.3	0.3 ± 0.3

Notes: Minor amounts of grand fir, lodgepole pine, and western larch are combined as "other." Data for 1998 (pretreatment), 2001, and 2004 are from fixed plots at uniformly spaced grid points.

TABLE 3. Density distribution of dead ponderosa pine and Douglas-fir by diameter at breast height (dbh) size class before and after four restoration treatments in northeastern Oregon, USA.

Species, year, and treatment	No. dead trees, by dbh class (cm)					
	Seedlings	<9.9	10–24.9	25–39.9	40–54.9	>55
Ponderosa pine						
1998						
Control	3.1	5.1	19.0	2.9	0.0	1.2
Burn	2.3	2.8	6.5	0.5	0.6	0.5
Thin	16.3	44.5	17.1	4.3	0.0	0.5
Thin + burn	1.5	3.6	7.7	1.3	0.0	0.0
2001						
Control	33.3	8.5	12.1	2.4	1.0	0.6
Burn	18.4	24.5	5.6	1.4	0.0	0.0
Thin	22.5	36.7	11.6	2.3	0.0	0.3
Thin + burn	54.6	20.9	9.3	1.0	0.0	0.0
2004						
Control	1.3	4.7	5.1	1.2	0.1	0.2
Burn	6.3	24.8	9.3	3.2	0.3	0.3
Thin	9.1	31.5	8.7	1.6	0.0	0.5
Thin + burn	3.7	12.8	14.6	6.0	0.4	0.0
Douglas-fir						
1998						
Control	1.1	30.2	8.1	0.7	0.0	0.0
Burn	0.0	0.4	0.0	0.0	0.0	0.0
Thin	0.4	18.3	4.2	0.0	0.0	0.0
Thin + burn	0.4	5.2	0.0	0.0	0.0	0.0
2001						
Control	4.8	26.6	12.3	0.0	0.0	0.2
Burn	7.7	1.0	1.0	0.0	0.0	0.0
Thin	8.4	20.6	1.6	0.0	0.0	0.0
Thin + burn	2.9	16.2	1.1	0.4	0.0	0.0
2004						
Control	1.2	20.4	15.5	0.0	0.7	0.0
Burn	3.3	3.8	0.5	0.2	0.0	0.2
Thin	6.0	15.9	3.0	0.2	0.3	0.0
Thin + burn	1.1	12.7	3.2	0.4	0.0	0.3

Pretreatment dead ponderosa pine consisted mostly of saplings (< 9.9 cm dbh) and trees in the 10–24.9 cm dbh size class (Table 3). Thin units contained a disproportionately higher number of dead seedlings and dead trees in the 25–39.9 cm dbh size class. After treatment, the density of dead ponderosa pine seedlings and saplings in the 0.1–9.9 cm dbh size class increased across all treatments, especially in the control, burn and thin + burn treatments. Density of dead saplings in the 0.1–9.9 cm dbh size class increased from 1998 to 2001 in burn and thin + burn units. Density in the larger size classes remained essentially unchanged. By 2004 density of dead ponderosa pine seedlings was similar to pretreatment levels. Density of dead ponderosa pine seedlings in burn units increased from pretreatment levels about ten-fold, and density in thin + burn units increased about four-fold. In both the 10 to 24.9 cm dbh and 25.0 to 39.9 cm dbh size classes, dead ponderosa pine density increased in burn and thin + burn units and decreased in thin units.

Fewer dead Douglas-fir occurred before treatment compared to ponderosa pine, and these dead consisted mostly of saplings ≤9.9 cm dbh and trees in the 10–24.9 cm dbh size class in control and thin units and saplings in thin + burn units (Table 3). Burn units contained few dead Douglas-fir in any size class. After treatment, density of dead Douglas-fir seedlings increased across all treatments, most notably in the burn and the thin treatments. Density of dead Douglas-fir saplings also increased in the thin + burn units. Dead Douglas-fir were absent in the larger tree sizes across all treatments in 2001. By 2004, density of dead Douglas-fir remained clustered in the seedling, 0.1–9.9 cm dbh, and 10.0–24.9 cm dbh size classes. Compared to pretreatment densities, treatments resulted in more dead seedlings in burn and thin units, more dead in the 0.1–9.9 cm dbh size class in burn units, and more dead in the 10.0–24.9 cm dbh in control and thin + burn units in 2004. Dead Douglas-fir were absent in the larger tree sizes across all treatments.

We identified seven causal agents of new tree mortality (Table 4). Direct mortality from fire was detected only in 2001 and 2002. This estimate of tree mortality from fire does not account for tree loss from consumption by fire or downfall. A regional wind event during the 2002–2003 winter months resulted in broken tops, uprooting, and dispersed tree mortality across all treatments. Within the study area, wind-caused mortality was more frequent in

TABLE 4. Density (no./ha) of newly dead trees (mean ± SE) by mortality agent after four fuel reduction treatments in northeastern Oregon.

Treatment	Fire	Wind	Western pine beetle	Mountain pine beetle	Pine engraver beetle	Red turpentine beetle	Wood borer
2001							
Control	0	0	0	0	0	0.38 ± 0.22	0
Burn	4.15 ± 2.69	0	0	0.02 ± 0.02	0	6.95 ± 2.20	0
Thin	0	0	0	0	0	0.55 ± 0.15	0
Thin + burn	3.91 ± 2.12	0	0.12 ± 0.12	0.08 ± 0.06	0	16.49 ± 9.69	0
2002							
Control	0	0	0	0	0.03 ± 0.03	0	0.07 ± 0.07
Burn	1.04 ± 1.04	0	0.12 ± 0.08	0	0.10 ± 0.07	0.03 ± 0.03	0.61 ± 0.30
Thin	0	0	0.04 ± 0.03	0	0	0	0.14 ± 0.10
Thin + burn	2.80 ± 2.8	0	0.06 ± 0.04	0	0.39 ± 0.24	0.06 ± 0.06	0.97 ± 0.49
2003							
Control	0	0.23 ± 0.13	0	0.05 ± 0.03	0.02 ± 0.02	0	0
Burn	0	0.17 ± 0.17	0.02 ± 0.02	0	0.03 ± 0.03	0	0.07 ± 0.05
Thin	0	0.44 ± 0.13	0	0	0	0	0.03 ± 0.03
Thin + burn	0	0.04 ± 0.03	0.02 ± 0.02	0	0	0	0.04 ± 0.02
2004							
Control	0	0	0	0.02 ± 0.02	0.10 ± 0.06	0	0.04 ± 0.04
Burn	0	0	0.07 ± 0.05	0.07 ± 0.07	0.07 ± 0.05	0.03 ± 0.03	0.05 ± 0.05
Thin	0	0	0.02 ± 0.02	0	0	0	0
Thin + burn	0	0	0.02 ± 0.02	0	0.02 ± 0.02	0	0

units with greater exposure along ridges. Mortality attributed to the western pine beetle was limited to the actively-treated units and was most frequent in thin + burn and burn units. Pine engraver beetles were not responsible for any tree mortality until 2002, when they began killing trees in all but the thin treatment. The red turpentine beetle was a key driver of tree mortality in burn and thin + burn units through 2001. Wood borer-caused mortality first appeared in 2002 and was most frequent in burn and thin + burn units, although it occurred across all treatments.

Plot-level mortality patterns

Mortality associated with all categories of causal agents was found to be highly variable at the level of experimental units. Many factors likely contributed to this, including the highly contagious nature of tree stands and cohorts, the patchiness of fuels and fire behavior, the mosaic of environmental conditions, and the stochastic nature of bark beetle infestations that occur at the unit scale. For these reasons, we examined tree mortality by considering the frequency with which mortality associated with a causal agent occurred in sample plots within units. For example, 21 of the 380 plots contained mortality of large trees attributed to wood borers, yet these plots were not uniformly distributed among treatments (Table 5). A significant discrepancy between expected and observed mortality associated with each treatment was detected ($\chi^2 = 24.74$, $P < 0.0001$), and mortality of large trees attributed to wood borers was conspicuously overabundant in the burn and thin + burn treatments. We repeated this test for both large and small trees for all causal agents (Table 6). The frequency of mortality of large trees attributed to wood borers and all bark beetles was higher than expected ($P < 0.001$). Similarly, the frequency of mortality of small trees attributed to fire, pine engraver beetle, wood borer, and all bark beetles was more frequent than expected ($P < 0.002$) in the burn and thin + burn treatments.

Structural equation modeling results

Burn and thin + burn treatments differed ($P < 0.001$) in woody fuel mass, maximum fire temperature, and surface fire severity (Table 7). Selected bivariate relations among measured variables were examined (Fig. 3) for significant nonlinearities and nonlinear models were not found to be significant improvements over linear approximations. Linearity was also examined in the structural equation model by adding quadratic and interaction terms to determine if the made significant contributions. After removing pathways that were determined to be nonsignificant, the resulting

TABLE 5. Frequency analysis of large-tree mortality from wood borers that occurred in individual sample plots after four fuel reduction treatments in northeastern Oregon.

Treatment	Condition	No. plots: Without large-tree mortality	No. plots: With large-tree mortality
Control	observed	78	0
	expected	74	4
Thin	observed	101	1
	expected	96	6
Burn	observed	92	5
	expected	92	5
Thin + burn	observed	88	15
	expected	97	6
Total		359	21

Note: Analysis based on Fisher's exact test produced a χ^2 of 24.74, with $P < 0.0001$ for no difference among treatments.

TABLE 6. Summary of tests for frequency of mortality from causal agents for large (≥25.0 cm dbh) and small (≤24.9 cm dbh) trees in burned and unburned sample plots in northeastern Oregon.

Causal agent	χ^2	Fisher's exact test P
Large trees		
Fire	3.29	0.35
Wind	1.54	0.75
Western pine beetle	0.78	1.00
Mountain pine beetle	0.00	0.06
Pine engraver beetle	4.84	0.19
Red turpentine beetle	8.13	0.06
Wood borer	24.70	<0.001
All beetles	31.84	<0.001
Small trees		
Fire	17.32	<0.001
Wind	4.22	0.26
Western pine beetle	2.92	0.46
Mountain pine beetle	3.88	0.21
Pine engraver beetle	14.08	0.002
Red turpentine beetle	1.81	0.85
Wood borer	25.06	<0.001
All beetles	31.30	<0.001

Note: In all cases, the ratio of observed to expected mortality was higher in burned compared to unburned plots.

model (Fig. 4) was found to have an overall χ^2 of 7.86 with a P value of 0.10, indicating reasonably close fit of data to model (note that in SEM, a nonsignificant P value means there are no major discrepancies between model and data). For probit-based models such as this one, which estimates effects of factors on the underlying probabilities of mortality, model degrees of freedom are estimated according to a formula developed by Muthén (1984). In this case, the estimated model degrees of freedom was 4.

Describing model results (Fig. 4) from right to left in the diagram, for large trees, only mortality from wood borers and from western pine beetles could be related to fire severity measures, with wood borers showing a stronger relationship (β or standardized path coefficient $= 0.89$, $R^2 = 0.80$) compared to western pine beetles ($\beta = 0.44$, $R^2 = 0.19$). Standardized path coefficients reflect the degree to which observed variation in one variable relates to observed variation in another variable. For small trees, mortality due to pine engraver beetle, wood borers, and other causes (including fire and physical damage), was related to fire severity. Physical damage to trees, such as bark scarring by harvesting equipment, contributed to mortality.

SEM results (Fig. 4) indicated that fire severity effects on trees could be associated with surface fire severity and tree charring. The presence of significant paths from surface fire severity and tree charring to the composite variable called fire severity indicated that these two different measures of fire severity contributed in unique ways to explaining mortality responses. Both surface fire severity and tree charring were greater where higher fire temperatures were recorded, although the relationships were only modestly strong ($\beta = 0.40$, $R^2 = 0.16$ for surface fire severity and $\beta = 0.29$, $R^2 = 0.08$ for tree charring). Higher fire temperatures were found to be associated with greater woody fuel mass. One-hundred hour fuels were more abundant in plots located in thin + burn treatments, and thus, there was an indirect linkage from treatment to fuels to fire temperatures to fire severity to mortality.

DISCUSSION

We found relatively low levels of delayed mortality within the first four to six years after our fuel reduction and restoration treatments in low-elevation dry ponderosa pine and Douglas-fir forests in northeastern Oregon. Delayed changes in forest structure after thinning, burning, and the combination of thinning and burning were minor compared to those reported after stand-replacement wildfires (Passovoy and Fulé 2006, McIver and Ottmar 2007) and after similar treatments in other forest ecosystems (McHugh and Kolb 2003, Stephens and Moghaddas 2005, Schwilk et al. 2006). Over 80% of the observed new mortality occurred the first year after treatment. Little additional mortality occurred in subsequent years: only 1% of the total mortality was added the last year of observation. This decline in tree mortality suggests that stands stabilized a few years after treatment, similar to mortality in pure ponderosa pine forests in the southwestern United States (McHugh et al. 2003) and much quicker than reported recovery after underburning in mixed-conifer forests in the Sierra Nevada (Schwilk et al. 2006). While the treatments were considered an operational success with respect to fuel reduction (Youngblood et al. 2008), the low levels of delayed mortality indicate that the subtle treatment effects were within the range of natural disturbances that occur in similar northeastern Oregon forests.

Mortality agents

Wind was the greatest cause of new mortality in large trees. Mortality from wind is a highly unpredictable process. Manipulation of stand density, especially in dense stands, may lead to wind-caused mortality or damage when storm events occur before newly thinned stands have established wind-firmness. We assumed most if not all of the wind-caused mortality occurred during a single storm event because of the direction of fallen tops and snapped boles. Mortality from wind was higher in control, burn, and thin units compared to thin

TABLE 7. Plot-level differences (mean ± SE) for 100-hour fuel mass, 1000-hour fuel mass, maximum temperature of the fire, and surface fire severity associated with two fuel reduction treatments in northeastern Oregon.

Parameter	Thin	Thin + burn
100-h fuel mass (Mg/ha)	2.40 ± 0.33	5.71 ± 0.32
1000 h fuel mass (Mg/ha)	1.05 ± 0.89	6.68 ± 1.11
Temperature (°C)	83.58 ± 8.24	125.99 ± 8.20
Severity (%)	4.68 ± 1.17	11.53 ± 1.14

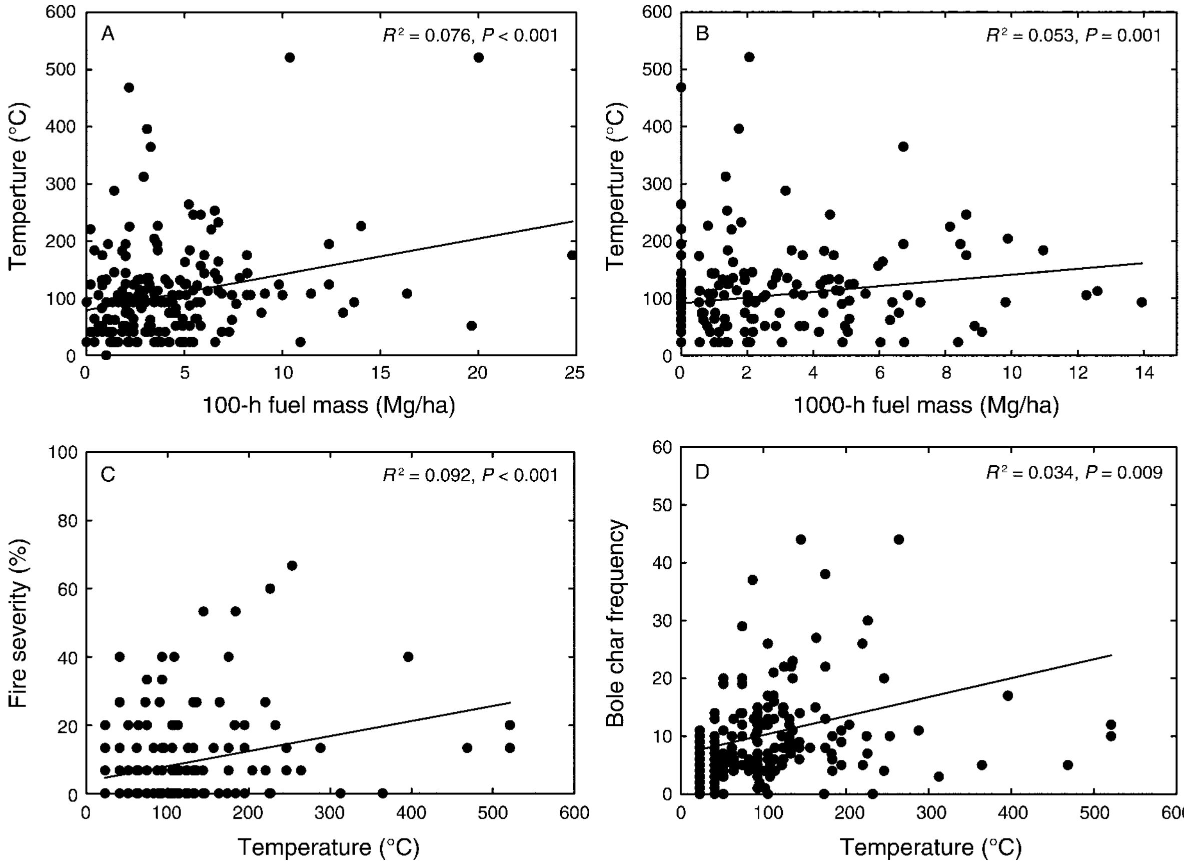

FIG. 3. Bivariate relationships used to predict tree mortality after burn and thin + burn fuel reduction treatments in northeastern Oregon: (A) 100-hour fuels are woody fuels between 2.54 and 7.62 cm in diameter; (B) 1000-hour fuels are woody fuels between 7.62 and 22.86 cm in diameter. Two data points with higher 1000-hour fuels are not graphed but were included in the analysis. Temperature is the mean maximum temperature recorded by pyrometers at 0.3 and 1.2 m above the forest floor. (C) Fire severity is the percentage of surface area of mineral soil exposed. (D) Bole char is the number of stems with bole char in each plot.

+ burn units, and also occurred outside the treatment units along ridges and windward slopes. Wind-caused mortality was not greater in burn units compared to unburned units (Table 4), despite potential damage to root systems and tree boles during the burning. Wind-caused mortality was likely related to topographic position and not to treatments that reduced stand density.

Fire was the greatest cause of mortality in small trees (exclusive of the impacts of harvester and forwarder equipment). Small Douglas-fir have thin bark, low branches, and fine needles that easily carry flames into crowns and are easily killed by fire. Small ponderosa pine also are susceptible to fire, but become increasingly tolerant with age as bark thickness increases and lower crown height increases. Large ponderosa pine, however, may become more susceptible to direct mortality from fire as size (diameter) increases, because interactions among previous injuries allow fire to kill a greater portion of the live cambium, fuels accumulate near the base of the tree and lead to higher fire intensity near roots and cambium, and carbohydrate levels decline because of preexisting stress (McHugh and Kolb 2003). Research on ponderosa pine in drier portions of northeastern Oregon suggests that the probability of mortality increases logarithmically with needle loss after fire, but increases linearly with bole char (Thies et al. 2006).

Total bark beetle-caused tree mortality across all species was only 0.03%, a level of mortality consistent with longer-term observations in northern Arizona (Zausen et al. 2005). While this overall percentage was low, mortality from bark beetles was more frequent in burn and thin + burn units and nearly absent from control and thin units. We made no attempt to monitor actual bark beetle population levels, e.g., through the use of pheromone-baited traps.

We noted a relatively high number of ponderosa pine killed in burn and thin + burn units for which mortality was attributed to red turpentine beetle (Table 4). Red turpentine beetle are known to attack the base of ponderosa pine that are fire-damaged, stressed, weakened, dying, or dead (Furniss and Carolin 1977, Mitchell and Martin 1980, McHugh et al. 2003, Short and

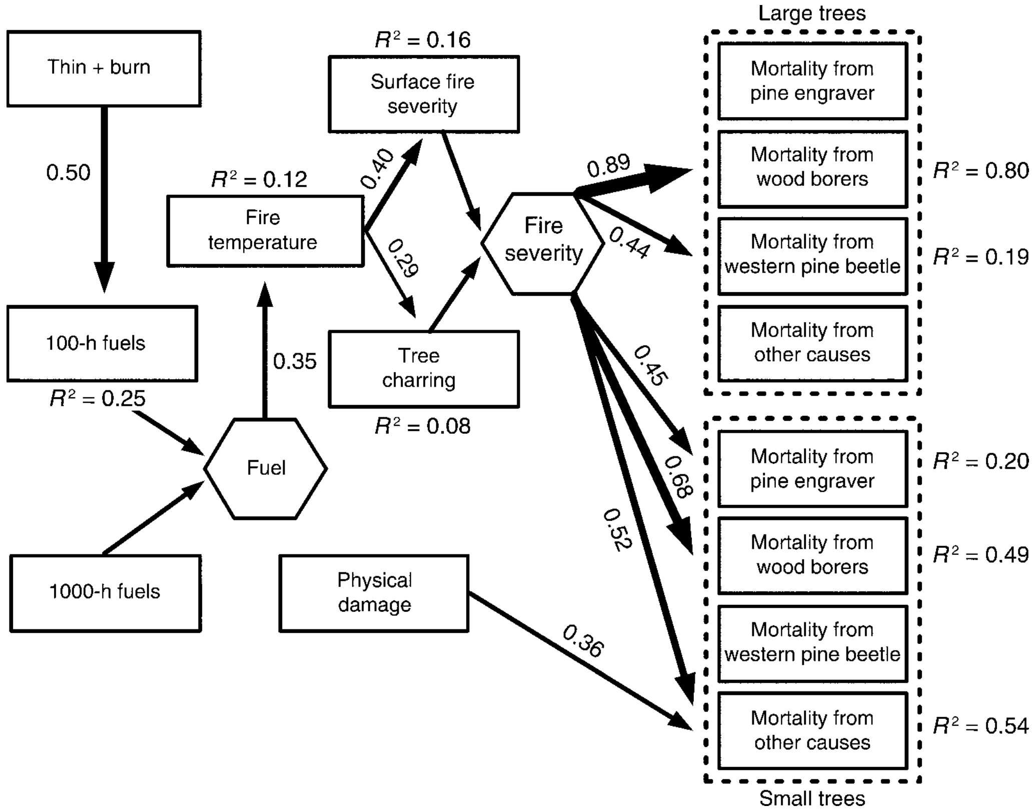

FIG. 4. Structural equation model results for large and small ponderosa pine mortality. Overall model $\chi^2 = 7.86$ with $P = 0.10$, indicating no major deviations between data and model. Rectangles represent observed variables, while hexagons represent composites summarizing the effects of multiple predictors on individual responses. Only significant pathways are shown. Path coefficients presented are standardized values. Observed variables with pseudo-R^2 values are response variables for mortality.

Negrón 2003). They also attack trees that are under attack by other bark beetles, such as western pine beetle (Fettig et al. 2004). Attacks typically do not lead to tree mortality. Tree mortality, however, was attributed to red turpentine beetle in a 17-year-old ponderosa pine plantation in northern California (Rappaport et al. 2001), in stands where logging residues were chipped and retained on-site in northern California (Fettig et al. 2006), and in a native pine of China after accidental introduction (Cognato et al. 2005). Until these recent reports, red turpentine beetle was not considered a primary mortality agent by most investigators. We recorded a high number of trees, especially in thin + burn units, with crown indications of physiological stress and the lower bole colonized by red turpentine beetle, yet they apparently regained vigor. Red turpentine beetle also attacked trees in burn and in thin + burn units and these trees failed to regain vigor and succumbed to the accumulated stresses. The majority of tree deaths attributed to red turpentine beetle were recorded in 2001; 12 months after the burns were conducted. Tree mortality also was attributed to red turpentine beetle in control and thin units where fire was not a precursor. Our methods prevented us from detecting possible wood borer activity at and above the midbole. Thus, some mortality attributed to red turpentine beetle may be the result of wood borer galleries higher along the bole then we detected. Our work, however, suggests that red turpentine beetle plays a stronger role as an agent of tree mortality in this portion of its distribution than previous work has indicated, and supports recent work in Arizona and California indicating that infestations of red turpentine beetle can result in ponderosa pine mortality (Ganz et al. 2003, Fettig et al. 2006).

Wood borers were the next most common tree-killing insect after the red turpentine beetle. No tree mortality was attributed to wood borer until 24 months after the fire, indicating that wood borer-caused mortality was delayed and indirect, and associated with burning (Table 4). New mortality in all treatments was attributed to wood borer colonization, although the frequency of mortality was related to burn and thin + burn treatments for both small and large trees (Table 6). Wood borer attacks can enhance fire-caused mortality, and wood borers can move from fire-damaged trees to attack adjacent undamaged trees (Short and Negrón 2003; but see Parker et al. 2006). Working in southeastern British Columbia on unreplicated treatments, Machmer (2002) reported that wood borers increased after burn, harvest and burn, and harvest treatments compared to two control units. In northern California, wood borers are considered secondary insects that follow the attack of western pine beetle and largely ignore trees mechanically killed by girdling (Shea et al. 2002). In our work, wood borers killed trees independent of western pine beetle. Wood borers are commonly known for their contribution as a food source for woodpeckers and their contribution in introducing wood decay fungi (Mitchell and Martin 1980). Our work suggests that wood borers may be an important tree-killing agent after fire in other northeastern Oregon ponderosa pine forests.

Fewer trees were killed by pine engraver beetle than wood borers. Mortality from pine engraver beetle was greater in small trees in burn and thin + burn treatments than in unburned treatments (Table 6). This same relation did not extend into larger trees. Pine engraver beetle are known to colonize fresh logging slash, the lower boles of small-diameter trees, and the upper boles of large-diameter trees that are stressed or injured. Our thin treatment was conducted during the summer of 1998 when pine engraver beetle would be expected to be in flight. Treatment prescriptions that defined minimum merchantability standards (13 cm diameter), however, precluded the creation of fresh slash of desirable diameter. Logging slash of this size created in one year is generally not suitable for colonization by pine engraver beetle the next year. Thus, our low number of trees killed by pine engraver beetle and their detection beginning in 2002 suggests that these beetles were at low population levels at the time of treatment and any that did develop in slash did not move into living trees.

Surprisingly, there were few instances of tree mortality attributed to western pine beetle. Western pine beetle are known to attack ponderosa pine with severe crown scorch during the growing season (McHugh et al. 2003). These beetles are attracted to large diameter ponderosa pine by tracking finely dispersed pheromone plumes that may be driven by stand density, atmospheric stability, wind, and humidity (Thistle et al. 2004). Their ability to colonize is positively related to crown scorch because the physiological condition of the tree crown influences resin production (Wallin et al. 2003). Apparently the degree of crown scorch that occurred as a result of our treatments was sufficient to allow successful colonization by some western pine beetles, yet the season of treatment and low levels of crown scorch contributed to keeping the overall level of tree mortality attributed to western pine beetle relatively low.

We noted few instances of delayed mortality attributed to mountain pine beetle. Fire-damaged ponderosa pine are susceptible to mountain pine beetle (Parker et al. 2006). Mortality in ponderosa pine attributed to mountain pine beetle has been positively correlated with high stand density (Sartwell and Dolph 1976, Fettig et al. 2007). Thinning has been shown to reduce the amount of ponderosa pine mortality caused by mountain pine beetle unless surrounding areas are allowed to develop epidemic population levels (Fettig et al. 2007). The mountain pine beetle often kills extensively when contiguous stands or landscapes become vulnerable. The variation in stand density and heterogeneity of structure across the landscape supporting our treatment units likely contributed to low susceptibility of delayed mortality attributed to mountain pine beetle.

Cascading effects

Questions about cascading effects, direct vs. indirect influences, and the roles of multiple factors are often difficult to address using univariate analyses (e.g., ANOVA) or descriptive multivariate methods (e.g., discriminant analysis, canonical correspondence analysis). SEM permitted consideration of hypotheses about how multiple processes may have collective and interconnected influences. We applied probit modeling within SEM to examine how the underlying (latent) probabilities of mortality were related to treatments, fuels, fire intensity, and fire severity. Our initial conceptual model (Fig. 1) suggests a large number of possible direct and indirect effects. The data support a relatively simple model in which treatment effects cascade along an indirect path through fuels, fire intensity, and fire severity to impact tree mortality. In the process of arriving at this model, we rejected a number of more complex, competing alternatives by finding that the data are inconsistent with such interpretations. SEM allowed us to make inferences that relate more directly to the processes of biological interest. We also were able to discern which measures or indicators of major factors were the most sensitive at detecting the signals connecting treatments with mortality, thus also informing us about measurement issues.

The effects of the thin and the thin + burn treatments on ponderosa pine mortality (Fig. 4) can be understood through their effects on fuels, fire intensity, fire severity, and physical damage. Woody fuel mass in both 100-hour and 1000-hour size classes was higher in plots with ponderosa pine mortality compared to plots without ponderosa pine mortality. Thinning in the thin + burn treatment increased the mass of these large woody fuels, and the higher fuel mass led to higher fire intensity and ultimately greater pine mortality. Fire intensity at the plot level was not well predicted by all the fuel data available: woody fuel mass in the 100-hour and 1000-hour size classes were better predictors of fire temperatures compared to other fuel classes. For burned treatments, the thin + burn effect was entirely indirect through increased mass of 100-hour fuels. Our SEM identified two important aspects of fire severity. The first of these was surface fuel consumption, indicated by surface fire severity and measured by mineral soil exposure. The second was partial consumption of standing tree boles, indicated by charring and measured by the frequency of charred boles. Both surface fire severity and bole charring were related to the mean maximum temperature of the passing fire front. These two relations were not as well predicted as one might expect, possibly because of spatial incongruities between fuel accumulations and residual trees. Physical damage had equivalent effects in burn and thin + burn treatments. Physical damage predicted other mortality in small trees to a modest degree.

In general, bark beetle-caused tree mortality was strongly related to high levels of fire severity. This was true for wood borers in both large and small ponderosa pine. Mortality of small ponderosa pine from pine engraver and mortality of large ponderosa pine from western pine beetle were both related to higher values of fire severity. Mortality from other sources in large ponderosa pine was low and independent of treatments or covariates. Mortality of small ponderosa pine from other sources was somewhat more related to treatment effects. While physical damage was related to mortality of small ponderosa pine, fire severity was a stronger predictor.

Our results indicated a relatively simple cascade of effects. Comparison of the range of possible effects indicated in the conceptual model (Fig. 1) to those found in the SEM results (Fig. 4) suggests a clear and simple set of mechanisms whereby similar thin + burn treatments can lead to increased fire severity and a greater risk of beetle-caused mortality in large trees. We offer this cautionary note: while under the conditions of our study the overall level of mortality was low, under other conditions similar treatments may create a greater risk of mortality through this cascade of effects.

Treatment considerations

Silviculturists and ecologists throughout the western United States are increasingly being asked to design fuel reduction and restoration treatments for low-elevation landscapes that historically supported high frequency, low-severity fires. Each of the three active treatments represent initial steps in the process of restoring historical forest structure conditions and reestablishing ecosystem processes that may reduce the risk of uncharacteristically severe wildfire (Spies et al. 2006). Managers are cautioned to use our results as indicative of only the first in a series of planned treatments. It is unlikely that any single treatment or entry will mitigate the nearly eighty years of fire exclusion, grazing, and preferential harvesting of large diameter ponderosa pine. Thinning and burning are often used to reduce stand basal area and density of small trees, remove fire-sensitive trees, reduce accumulations of woody fuels, and create more fire-resistant forest structure. Thinning is designed to improve growth of the residual trees, to enhance forest health, or to reduce the risk of future tree mortality in immature forests. Thinning also may be used to develop or protect vertical and horizontal forest structure, to develop larger trees, snags, and down wood for terrestrial habitat, and to promote late-successional characteristics (Powell et al. 2001). We used a low thinning that removed lower canopy trees and retained larger codominant and dominant trees, aiming to mimic mortality caused by tree-to-tree competition or surface fires under historical conditions (Graham et al. 1999). Prescribed burning has been recommended as a primary means for reducing fuel mass, for controlling unwanted dense regeneration that serves as ladder fuels, for increasing forage production, for converting organically bound nutrients to forms more readily available for plant uptake, and for decreasing the risk of stand-replacement wildfire in low-elevation dry forests (Mutch et al. 1993, Harrington 1996). As a fuel reduction treatment, burning may have the desired attributes of being "natural" within the ecological system and may provide a full range of ecological effects because of varying intensities across burn units (Brown et al. 2004), yet is imprecise within the context of single tree effects. Our treatments were purposely applied as late season or fall burns because at this time woody fuels and associated vegetation moisture levels usually are lower than during early season or spring burning periods, and lower moisture levels enhance the uniform spread of fire. Also, a late season or fall burn most closely resembles wildfires that occurred under natural disturbance regimes (Heyerdahl et al. 2001). The thin + burn treatment is an increasingly common management tool, with the thin component providing structure control and the burn component providing heterogeneity in effects that more closely resembles natural disturbances. There is broad agreement that this combination should move forests in the direction of historical structures and disturbance regimes (Youngblood et al. 2004, Agee and Skinner 2005) and contribute to process-centered restoration goals (Falk 2006).

While reference conditions may describe the range of natural variation in composition and structure and may serve as criterion for measuring success of restoration treatments, we have little to guide the development of management scenarios to ensure that disturbance processes, other than fire, are fully incorporated. Late-successional reference conditions may not always serve as the best management goal, especially in the face of climate change uncertainty. Our active treatments may be initial steps in creating structures that are better able to resist the influence of climate change, are resilient to change, and yet enable response to change (Millar et al. 2007). Ponderosa pine stands with low fuel accumulations and stand structures that emphasize low densities and large tree diameters likely are better able to resist the undesirable or extreme effects of multiple disturbances. Stands with this structure, when dispersed across larger landscapes, may provide landscape-scale resiliency because they are better able to return to prior conditions after a disturbance while stands with higher fuel accumulations, higher density, and smaller trees may experience greater severity in disturbance during the same event. Finally, stands with this structure may respond favorably to change because they have been realigned to incorporate both current and expected natural disturbance processes.

Although thinning and burning are not new silvicultural practices in low-elevation forests, better information is needed about long-term ecological consequences of these treatments (Weatherspoon 2000, Fulé et al. 2007, McIver et al. 2008). Understanding of the linkages among fuel reduction and forest restoration treatments and the drivers of ecological processes are especially lacking. There is as yet no comprehensive comparison of treatment effects for low-elevation dry conifer forests of the western United States to guide decision-makers. Controlled operational-scale experiments such as those of the Fire and Fire Surrogate study, and continuation of observations beyond initial short-term effects, are essential for providing such comparison. Further work with additional treatments or greater pressure from bark beetles would aid in quantifying ecosystem resilience. When extended beyond this first set of treatments, our study provides a foundation for assessing the effects of continued long-term restoration treatments for reducing fuels and accelerating the development of late-successional stand structure in low-elevation dry ponderosa pine and Douglas-fir forests of northeastern Oregon.

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